ZooKeys 20: 175–214 (2009)
doi: 10.3897/zookeys.20.161
www.pensoftonline.net/zookeys

RESEARCH ARTICLE

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Description of three new genera and four new species of Neanastatinae (Hymenoptera, Eupelmidae) from Baltic amber, with discussion of their relationships to extant taxa

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Academic editor: *Norman Johnson* | Received 07 April 2009 | Accepted 27 July 2009 | Published 14 September 2009

urn:lsid:zoobank.org:pub:4B874175-CBAE-4497-87CD-C1E4EC113D43

Citation: Gibson GAP (2009) Description of three new genera and four new species of Neanastatinae (Hymenoptera, Eupelmidae) from Baltic amber, with discussion of their relationships to extant taxa. In: Johnson N (Ed) Advances in the systematics of Hymenoptera. Festschrift in honour of Lubomír Masner. ZooKeys 20: 175–214. doi: 10.3897/zookeys.20.161

Abstract

Aspidopleura baltica **gen. n.** and **sp. n.**, *Brevivulva electroma* **gen. n.** and **sp. n.**, *Neanaperiallus masneri* **gen. n.** and **sp. n.**, and *Metapelma archetypon* **sp. n.** are described in Neanastatinae (Chalcidoidea, Eupelmidae) from Baltic amber. New information is given on the morphology of *Eopelma* Gibson, *Lambdobregma* Gibson, *Metapelma* Westwood and *Neanastatus* Girault, the four extant genera previously classified in Neanastatinae, and the extinct and extant taxa are compared with other Chalcidoidea for hypotheses of character evolution and phylogenetic relationships. Structural features of *Neanaperiallus* and *Aspidopleura* indicate that except for a greatly enlarged acropleuron the groundplan structure of Neanastatinae was similar to male Eupelminae or some Cleonyminae (Pteromalidae). Furthermore, classification of *Neanaperiallus* in Neanastatinae results in no putative autapomorphies to support monophyly of the subfamily. Some features of Encyrtidae, Tanaostigmatidae and Neanastatinae suggest that the taxa may have had a common ancestor, therefore rendering Eupelmidae paraphyletic. A key to the seven recognized genera and a revised diagnosis of Neanastatinae are given.

Keywords

Eopelma, Lambdobregma, Metapelma, Neanastatus, Eupelminae, Calosotinae, *Savzdargia,* Encyrtidae, Tanaostigmatidae, Baltic amber

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Introduction

Neanastatinae is one of three subfamilies classified in Eupelmidae (Chalcidoidea). Kalina (1984) established Neanastatinae for *Neanastatus* Girault after Bouček (1958) had earlier subdivided Eupelmidae into Eupelminae Walker and his new subfamily Calosotinae. Unaware of Kalina's classification, Bouček (1988b) subsequently established the junior synonym Metapelmatinae for *Metapelma* Westwood and *Neanastatus*, and Gibson (1989) revised the world genera under the name Metapelmatinae. He included *Neanastatus*, *Metapelma*, and two new genera, *Eopelma* Gibson and *Lambdobregma* Gibson, in what is correctly Neanastatinae. Eight extant genera are classified in Calosotinae (Gibson 1989), whereas 33 genera are recognized in Eupelminae (Gibson 1995). Trjapitzin (1963) described *Propelma rohdendorfi* as a new genus and species of Eupelminae from Baltic amber, but Gibson (1995) synonymised *Propelma* under the extant genus *Eupelmus* Dalman. No fossil Neanastatinae or Calosotinae have previously been described.

Of the four genera comprising Neanastatinae, only *Metapelma* is known from all biogeographic regions. *Neanastatus* is restricted to the Old World, *Eopelma* to the Oriental Region, and *Lambdobregma* to tropical and subtropical regions of the New World as far north as Florida, USA (Gibson 1989). *Eopelma* and *Lambdobregma* are both monotypic although other undescribed species are known (Gibson 1989), whereas there are 37 valid species in *Metapelma* and 39 in *Neanastatus* (Noyes 2003). At least three of the genera have quite different host ranges. The hosts of *Eopelma* are unknown and the egg of a cricket (Orthoptera: Grylloidea) is the only reported host for *Lambdobregma* (Gibson 1989). Species of *Metapelma* are primary larval/pupal parasitoids of at least four families of wood-boring beetles (Bostrichidae, Buprestidae, Cerambycidae and Curculionidae including Scolytinae) and most species of *Neanastatus* are primary or hyperparasitoids of Cecidomyiidae (Diptera) gall-makers, though Gibson (1989) and Noyes (2003) list other rarely reported gall-making hosts.

Eupelmidae has long been proposed to form some sort of intermediate group or link between Cleonyminae (Pteromalidae) and Encyrtidae and/or Tanaostigmatidae though the monophyly of the family and its higher-level relationships with other Chalcidoidea remain unsubstantiated (Graham 1969; Bouček 1988a, 1988b; Gibson et al. 1999). This is because female Eupelminae and both sexes of Neanastatinae, Encyrtidae and Tanaostigmatidae share similar suites of conspicuously modified mesosomal features, whereas male Eupelminae exhibit mostly plesiomorphic features that closely resemble Cleonyminae, and some genera of Calosotinae are intermediate in structure between the two extremes (Gibson 1986, 1989). The similar suites of apomorphic features are thought to constitute functional-structural complexes to improve jumping ability and consist of structures that are modified either to increase power for jumping or to protect the body from the greater forces involved in jumping (Gibson 1986). Putative autapomorphies support the monophyly of Encyrtidae and Tanaostigmatidae sensu stricto (see Gibson 2008) but not Eupelmidae (Gibson 1989). The likely groundplan structure of Neanasta-

tinae includes some features that are shared with Calosotinae and Eupelminae but not with Encyrtidae and Tanaostigmatidae s. s., such as ventrally divergent eyes, an 8-segmented funicle with at most a single anellus, and protibial apical denticles. However, these features are shared also with Cleonyminae and therefore likely represent symplesiomorphies. Consequently, classification of Neanastatinae along with Calosotinae and Eupelminae in one family is primarily because they share some symplesiomorphic features and do not possess the apomorphic features that differentiate Encyrtidae or Tanaostigmatidae s. s. Although evidence for the monophyly of Eupelmidae is lacking and the family could constitute a paraphyletic or even polyphyletic grade-level taxon, Gibson (1989) proposed that each of the three subfamilies is monophyletic. He differentiated Neanastatinae from Calosotinae and Eupelminae by several features, including structure of the pronotum and a different mesotarsal peg pattern. Neanastatinae is further differentiated from Eupelminae by the absence of extreme sexual dimorphism, and from Calosotinae and female Eupelminae by the inability to rotate the mesocoxae out of their combined fossa (Gibson 1989, 2008).

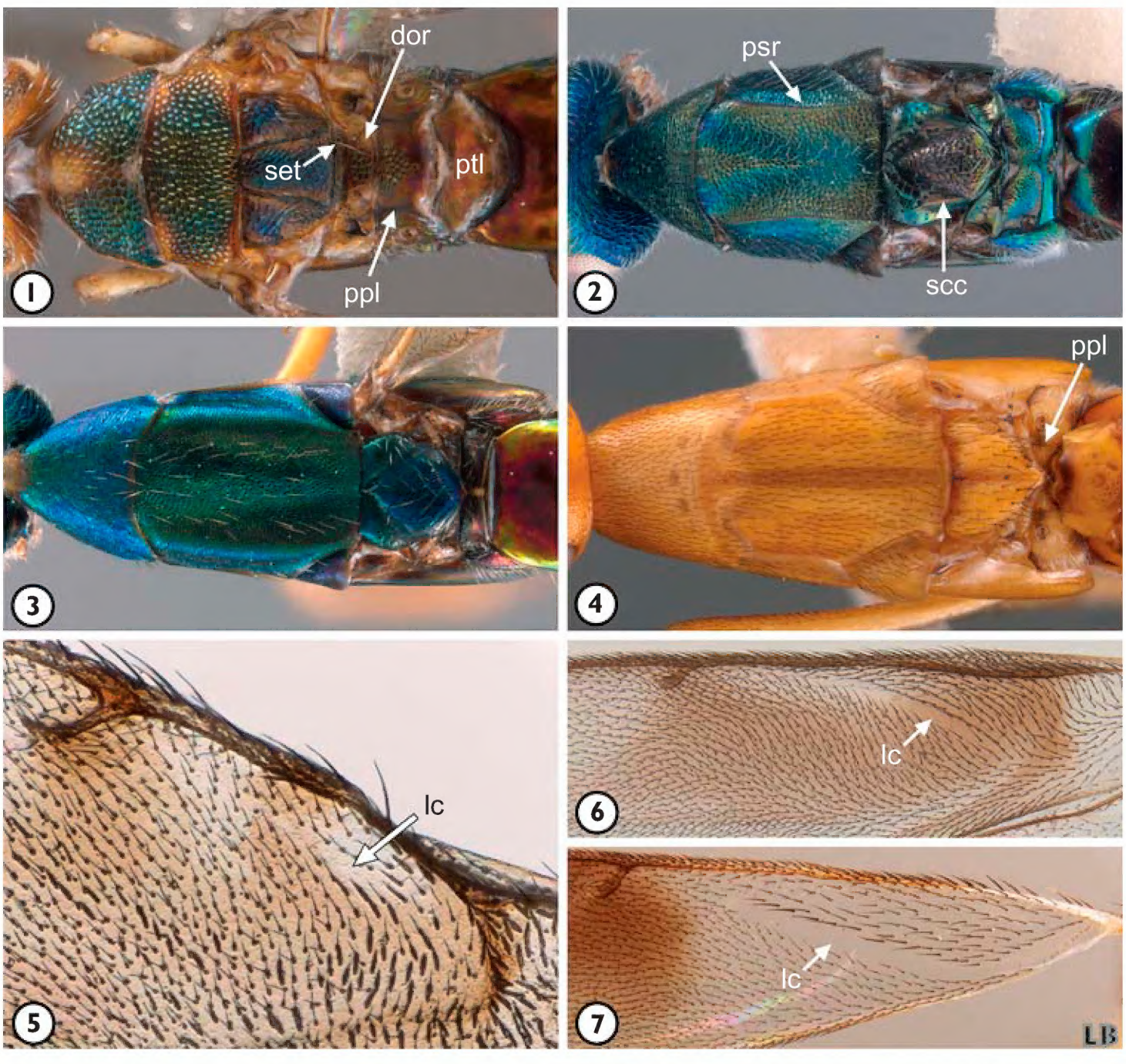
Resolving the monophyly and relationships of Eupelmidae, of its three subfamilies, and of other Chalcidoidea requires data derived from molecular analyses combined with comparative morphology of extant Chalcidoidea. The discovery and description of extinct taxa can provide additional information for phylogenetic analyses to help explain present day character-state distributions and biogeographic patterns. Several years ago I received inclusions of Baltic amber from Jens-Wilhelm Janzen, Seevetal, Germany. Included were seven specimens I described as *Leptoomus janzeni* in Tanaostigmatidae sensu lato (Gibson 2008) and four specimens that appeared to represent three new species of Neanastatinae. More recently, I received an additional Baltic amber specimen from the American Museum of Natural History (AMNH), New York, NY, USA, which, although poorly preserved, represents yet another new taxon. At least the latter specimen is from a Lutetian (Middle Eocene) amber deposit, which indicates a minimum age of about 42–49 million years and probably a maximum age of 54 million years (Keyser and Weitschat 2005). The purpose of this paper is to describe and compare the five Baltic amber specimens relative to extant Neanastatinae and other Chalcidoidea.

Materials and methods

Materials and methods, including the concept of Tanaostigmatidae sensu stricto and Tanaostigmatidae sensu lato, are as given in Gibson (2008). The combined generic and species descriptions are not rigorously comparable because the specimens differ in quality of preservation and the parts that are visible. New information on the structure of extant Neanastatinae is given prior to the description of the fossil taxa to supplement the generic descriptions of Gibson (1989) and to provide additional data for comparison of the extinct and extant taxa.

Neanastatinae

Diagnosis. Males and females not dimorphic in mesosomal and other secondary sexual features. Mesopleuron consisting of uniformly convex acropleuron (Figs 21, 22) or at most with a small flat region (Fig. 25: lep) between acropleuron and mesocoxa or a convex, subdivided region (Fig. 20: lep, uep) between acropleuron and metapleuron. Head with malar sulcus. Antenna with 6–8 funicular segments between pedicel and compact clava, including at most 1 ring segment (anellus). Pronotum variable in length, in dorsal view strongly transverse (Figs 49, 59) to elongate-subtriangular (Figs 1–4), but uniformly sclerotized without mediolongitudinal line. Mesoscutum sometimes with shallow furrow extending from anterior margin mesal to mesothoracic spiracle and/or with ridged parapsidal lines (Figs 2, 14: psr) differentiating median and lateral mesoscutal lobes, but without linear notauli. Lateral surface of prepectus



Figures 1–7. 1–4 dorsal mesosoma: **1** *Eopelma* sp. (♂, Thailand) **2** *Metapelma spectabile* Westwood (♂) **3** *Lambdobregma* sp. (♀) **4** *Neanastatus* sp. (♀) **5–7** fore wing: **5** *Eopelma* sp. (♂, Thailand) **6** *Lambdobregma* sp. (♀) **7** *Neanastatus* sp. (♀).

flat, in one extinct taxon extending anteriorly very slightly over posterolateral margin of pronotum (Fig. 60: pre), but not as a conspicuously projecting lobe. Mesothorax usually with variably large pit laterally between base of mesocoxa and angle formed between acropleuron and mesosternum (Figs 22, 26: mcc). Mesosternum with sulcate discrimen (Figs 24, 26: dsc), ventrally without distinct membranous region anterior to each mesocoxa. Mesotrochantinal lobes not externally exposed and in same plane as mesosternum. Mesocoxae inserted distinctly posterior to midline of acropleuron and unable to rotate anteriorly out of combined fossa. Metacoxae directed posteroventrally in oblique plane relative to mesosoma. Gaster with cercus not advanced conspicuously.

The above diagnosis assumes sexual dimorphism in the newly described extinct taxa was similar to extant genera of the subfamily.

Information on extant Neanastatinae supplemental to Gibson (1989). Since describing *Eopelma* (Gibson 1989), I have seen two additional males that represent two new species. A male from Borneo (Sabah) is similar to the unique female of *E. mystax*, whereas a male from Thailand is similar to the three males of the undescribed species I reported from Nepal. I described *Eopelma* as having the vertex and temples smoothly rounded into the occiput, but the vertex is extensively carinate between the eyes in the Borneo male (Fig. 23) and there is a slight indication of a transverse vertexal carina in the Thailand male. The head is ovoid in lateral view as in other *Eopelma* and all Neanastatinae except *Neanastatus*. In *Neanastatus* the head is lenticular in lateral view with the vertex completely carinate between the eyes (Gibson 1989, character 31, state 2; fig. 13). I also described *Eopelma* as lacking a fore wing hairless streak (= linea calva), but the fore wing of the Thailand male has a very short and slender, quite inconspicuous bare band behind its obliquely angled parastigma and base of the marginal vein (Fig. 5: lc). Other *Eopelma* have uniformly setose fore wings. Although some species of *Metapelma* also have uniformly setose fore wings, some have a distinct linea calva and others have a narrow, oblique band of setae behind the parastigma that point in a different direction from the other setae. This latter setal pattern suggests a linea calva that is secondarily 'filled' with setae, and presence of a distinct linea calva in some species of *Metapelma* indicates this as a groundplan feature of the genus. Gibson (1989, character 16, state 2) hypothesized that a linea calva was a groundplan feature of Neanastatinae that was secondarily lost from *Eopelma*. However, the presence of the very short fore wing bare band in the Thailand male may support a linea calva also as a groundplan feature of *Eopelma*. Gibson (1989) did not mention that in *Neanastatus* the linea calva is open below and extends to the base of the wing along the anal margin (Fig. 7: lc). Other extant Neanastatinae with a linea calva have it extending at most as far as the setose basal cell (Fig. 6: lc). *Neanastatus* also differs from other extant genera in having the propodeal spiracles adjacent to the anterior margin of the propodeum (Figs 17, 18), whereas in *Metapelma*, *Lambdobregma* and *Eopelma* the spiracles are near the midlength of propodeum or even nearer its posterior margin (Figs 11–16).

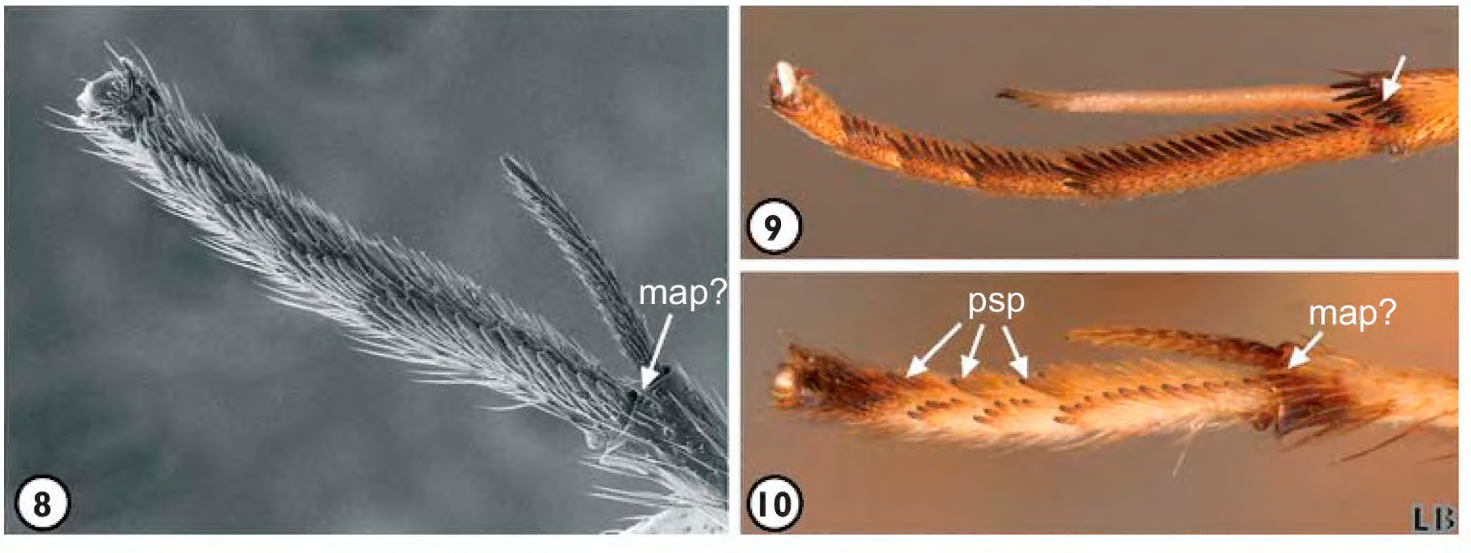
As described by Gibson (1989), *Eopelma* has autapomorphic structures of the scutellum, metanotum, propodeum and petiole (Figs 1, 11, 12) within Neanastatinae. The structure of its scutellar-axillar complex resembles that of Colotrechinae (Pteroma-

lidae) because subparallel grooves differentiate a median scutellar region from lateral regions that consist of the dorsal axillar surface anteriorly and the inclined axillula posteriorly (Figs 1, 11). Consequently, the uniform longitudinal grooves actually are composed of the scutoscutellar sutures anteriorly (Fig. 11: ssa) and the axillular sulci (Fig. 11: axs) posteriorly, with the posterior part of each scutoscutellar suture (Fig. 11: ssp) curved to the lateral margin of the complex as a much less distinct line that separates the dorsal axillar surface (Fig. 11: das) from the axillula (Fig. 11: axl) (compare Figs 11, 12 with Figs 13, 14). The scutellum is also bare except for a variable number of setae laterally plus quite a strong seta (Figs 1, 12: set) posterolaterally anterior to a transverse, flange-like scutellar margin rim (Figs 11, 12: smr). This scutellar setal pattern is most similar to that of *Lambdobregma*, which also has the posterior setae the longest and the setae restricted to narrow lateral bands or setal lines (Fig. 15), whereas *Metapelma* (Figs 13, 14) and *Neanastatus* (Figs 17, 18) have the scutellum much more extensively setose. Furthermore, the posteriorly rounded or angulate part of the scutellum in *Metapelma* and *Lambdobregma* has a very slender marginal rim (Figs 14, 16: smr) and that of *Neanastatus* a very short rim posterolaterally (Figs 17, 18: smr). These rims presumably are homologous with the more conspicuously flange-like, transverse scutellar margin rim in *Eopelma* (Figs 11, 12). *Neanastatus* is unique in having the axillar carina, which separates the dorsal and lateral axillar surfaces, developed more distinctly into a flange (Figs 17, 18: afd) than in other genera. Posteriorly, the flange is also projected at a right angle ventrally so that it extends as a vertical flange to the frenal arm (Fig. 18: afl, far) rather than angled evenly to the frenal arm (Fig. 16: axc, far) as in other extant Neanastatinae. This is a consequence of the dorsal surface of the unusually small axilla of *Neanastatus* being horizontal rather than inclined as for other genera that have comparatively much larger axillae.

Another unique feature of *Eopelma* in Neanastatinae is its transverse-rectangular metanotum exposed between the scutellum and propodeum, which has a reticulate dorsellum delineated by an anteriorly curved line (Figs 1, 11: dor). Except for *E. mystax*, the large propodeum also has a longitudinal line (Fig. 1: ppl) mesal to each propodeal spiracle, which differentiates a median plical and lateral callar regions. Gibson (1989) did not note that the much smaller propodeum of *Neanastatus* is also differentiated into a median and lateral regions by a longitudinal line (Fig. 4: ppl) mesal to each propodeal spiracle. Such lines are not apparent on the propodeum of *Metapelma* (Fig. 2) and *Lambdobregma* (Fig. 3), but using scanning electron microscopy they also are not visible on the propodeum of *Eopelma* (cf. Figs 1, 11) or *Neanastatus* (cf. Figs 4, 17). The lines therefore probably represent internal ridges that show through the comparatively light colored cuticle of *Eopelma* and *Neanastatus*. Their apparent absence from *Metapelma* and *Lambdobregma* might be because the propodeum of these two genera lack internal ridges or that they have the ridges but these do not show through the darker cuticle that characterizes the two genera. Gibson (1989) also stated that the plical region was bare in all genera of Neanastatinae; however, a few species of *Metapelma* have the plical region setose laterally near the propodeal spiracle and species of *Lambdobregma* with a dorsally subdivided scrobal channel have the plical

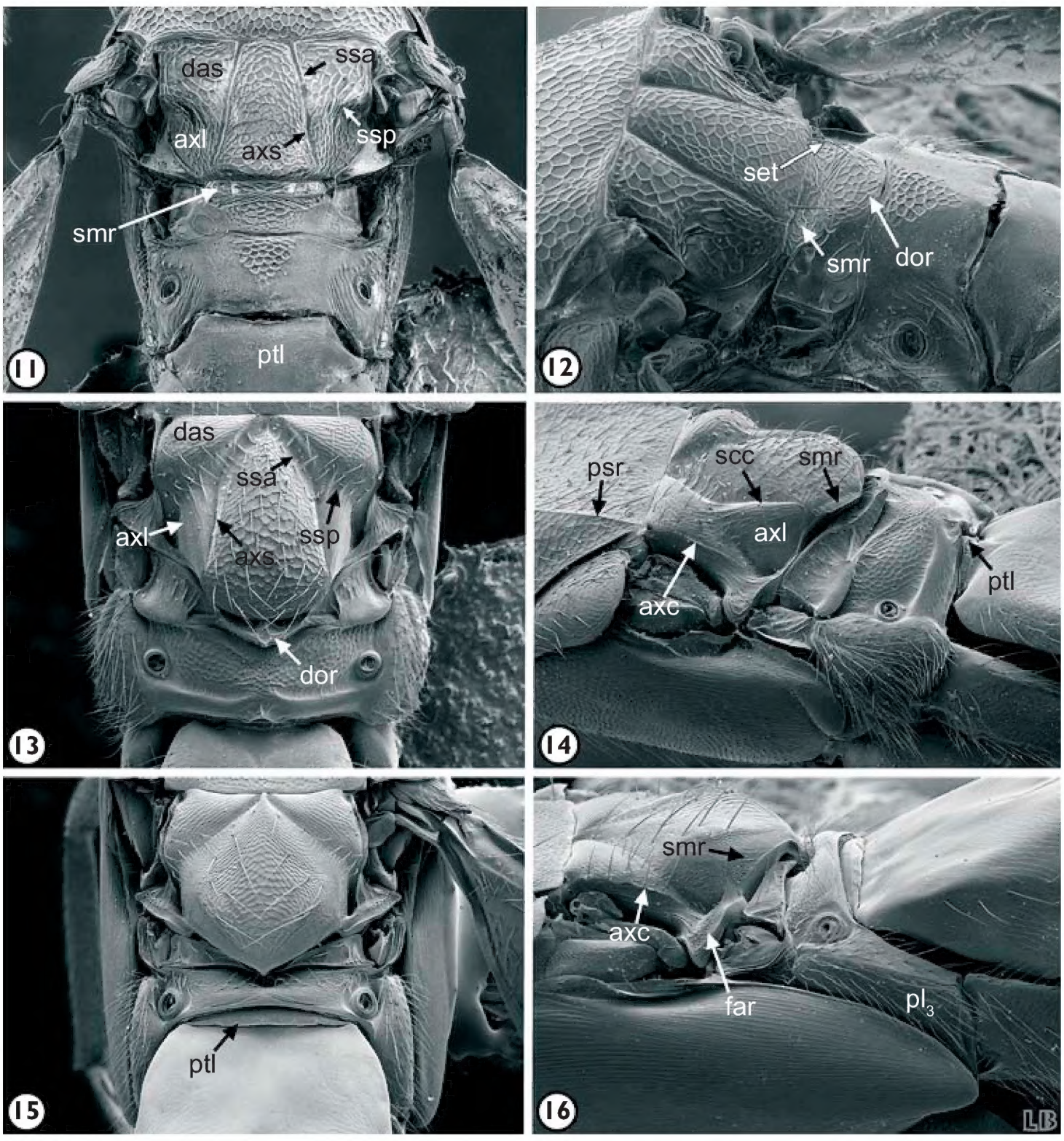
region extensively setose (Figs 15, 16). An undescribed species of *Lambdobregma* from Chile that has a single Λ-shaped rather than subdivided scrobal channel has the plical region bare except for a single seta close to the spiracle, which likely is the groundplan propodeal setal pattern for *Lambdobregma*. A laterally setose plical region is also likely a secondarily derived feature in *Metapelma*.

Mesopleural structure of *Eopelma* also differs from other Neanastatinae because the acropleuron is emarginate posteroventrally and there is a comparatively large flat region between it and the base of the mesocoxa (Figs 24, 26: lep). The position of this region is similar to that of the lower mesepimeron of Pteromalidae (Gibson 1986, fig. 2), male Eupelminae (Gibson 1986, fig. 1), and other chalcids that lack a completely enlarged acropleuron (Gibson 1986, figs 25–28). Other extant Neanastatinae have the posteroventral margin of the acropleural sulcus evenly curved and the acropleuron either extends to the mesocoxa (Figs 21, 22) or is separated from it by only a very slender region, such as in *Metapelma* (Fig. 19: mes). *Metapelma* differs from other Neanastatinae in having a horizontally subdivided, convex region (Figs 19, 20: uep, lep) between the acropleuron and metapleuron. The site of origin of three muscles (Gibson 1986, cf. figs 2, 8, 51, 52: muscles 12, 16, 19) support homology of this subdivided region as the upper and lower mesepimeron even though position of the region above the mesocoxa is anomalous and there is also a slender region between the acropleuron and base of the mesocoxa (Gibson 1986, fig. 51). Structure of the acropleural sulcus and setal pattern of the acropleuron are also unique for *Metapelma*. The acropleural sulci are directed anteroventrally from above each mesocoxa so that in ventral view they are convergent (Gibson 1989, fig. 93) and anteriorly there is a separate, oblique groove that extends toward the ventral angle of the prepectus (Gibson 1989, fig. 45). Furthermore, the acropleuron is partly setose above the two putative sections of the acropleural sulcus. Other extant Neanastatinae have the acropleural sulci directed straight forward from above each mesocoxa so that in lateral or ventral view they are parallel (Figs 22, 24, 26: acs; Gibson 1989, figs 92, 94) and anteriorly each sulcus is abruptly angled dorsally as a usually obscure, posteriorly curved groove or line that extends toward about the



Figures 8–10. Mesotarsus and tibial spur: **8** *Eopelma* sp. (♂, Borneo) **9** *Neanastatus* sp. (♀) **10** *Eopelma* sp. (♂, Thailand).

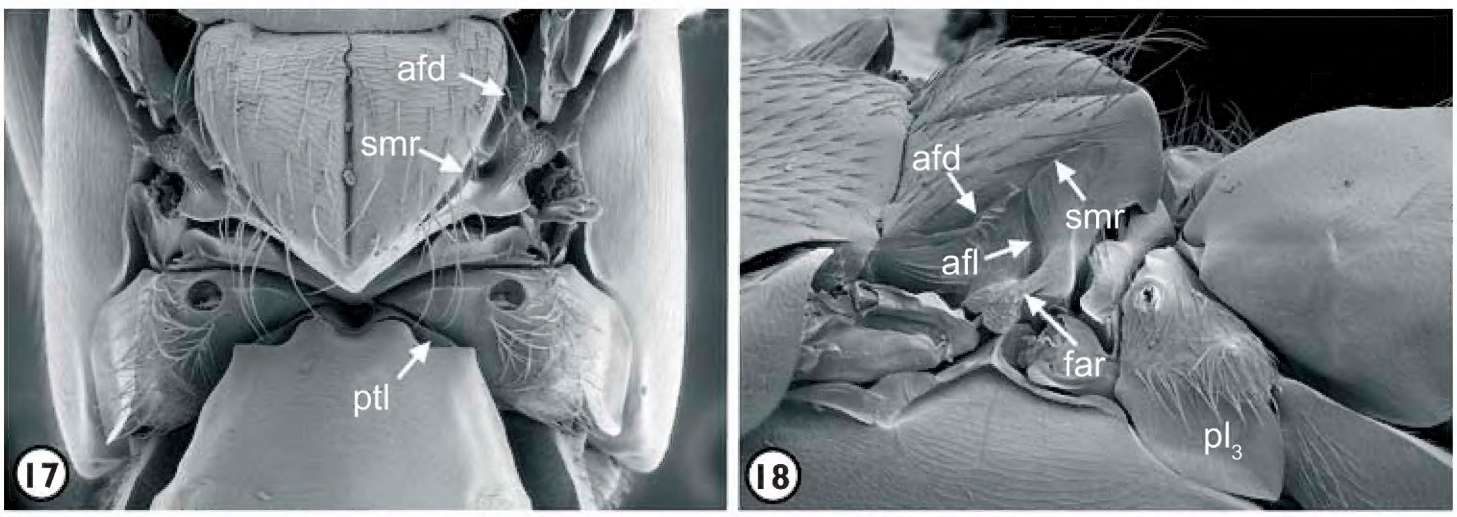
middle of the prepectus. Furthermore, the mesepisternum is setose only anterior to and ventral to the single acropleural sulcus and the acropleuron is completely bare. Other chalcids with an enlarged acropleuron also have a single acropleural sulcus and the acropleuron completely bare (see figs in Gibson 1989). The different mesopleural structures of *Eopelma* and *Metapelma* suggest different transformation series from some ancestor that had only a partially enlarged acropleuron and an exposed upper and lower mesepimeron anterodorsal to the base of the mesocoxa between the acropleuron and metapleuron. Among extant Eupelmidae, some Calosotinae have mesopleural structures similar to this hypothesized ancestral structure, including *Archaeopelma* Gibson (1986, fig. 25) and *Licrooides* Gibson (1986, fig. 26). Furthermore, *Paraeu-*



Figures 11–16. Scutellar-axillar complex to base of gaster, dorsal and dorsolateral view, respectively: **11, 12** *Eopelma* sp. (♂, Thailand) **13, 14** *Metapelma spectabile* Westwood (♂) **15, 16** *Lambdobregma* sp. (♀).

sandalum chilense Gibson has a large, flat, lower mesepimeron between the base of the mesocoxa and the acropleuron (Gibson 1986, fig. 27) as well as a very slender band (upper mesepimeron) dorsally between the acropleuron and metapleuron, which is distinguished from the lower mesepimeron by a shallow horizontal furrow. Because of the angle of view, the upper mesepimeron is not visible in Gibson (1986, fig. 27).

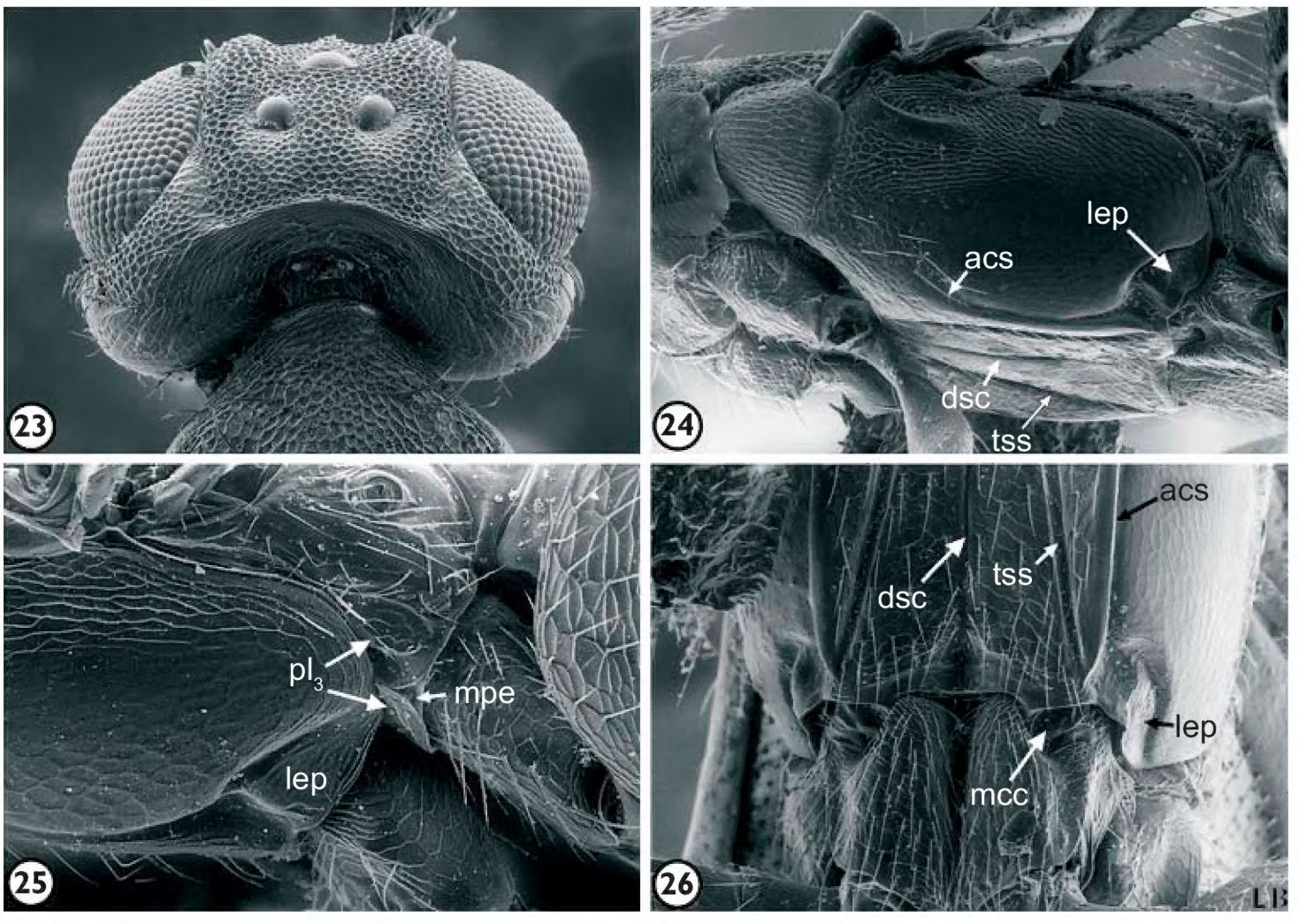
The pleural structure of *Eopelma* differs further from other extant Neanastatinae because there are two small sclerites between the posterior margin of the mesopleuron and the metacoxa (Figs 24, 25: pl_3). There is a small, more or less triangular, bare or very sparsely setose dorsal region between the acropleuron and the anterodorsal angle of the metacoxa, and a more elongate, bare or very sparsely setose region between the acropleu-



Figures 17–22. 17, 18 *Neanastatus* sp. (♀), scutellar-axillar complex to base of gaster: **17** dorsal view **18** dorsolateral view. **19, 20** *Metapelma spectabile* (♂): **19** lateral mesosoma **20** apex of acropleuron to propodeum, lateral view (setae from metapleuron removed). **21–22** lateral mesosoma (♀): **21** *Lambdobregma* sp **22** *Neanastatus* sp.

ron/lower mesepimeron and the anteroventral margin of the metacoxa. In *Metapelma*, the uniformly setose metapleuron (Figs 19, 20: pl_3, setae removed) extends between the mesepimeron and the metacoxa to the base of the mesocoxa. Its anterior margin has a variably distinct emargination or suture (Fig. 20: mpe) where the posterodorsal margin of the lower mesepimeron originates. The emargination interdigitates with the mesepimeral margin, apparently to limit slight movement between the two sclerites. Comparison of this structure with that of *Eopelma* suggests that the ventral sclerite between the acropleuron and metacoxa likely represents a secondary subdivision of the metapleuron, even though the emargination extends from the posterior margin of the metapleuron in *Eopelma* (Fig. 25: mpe) and from its anterior margin in *Metapelma* (Fig. 20: mpe). In *Lambdobregma*, the metapleuron superficially appears as an elongate, setose region above the posterodorsal margin of the acropleuron (Fig. 16: pl_3), but it continues ventrally to the anteroventral angle of the metacoxa as a very slender bare strip that is concealed in lateral view by the acropleuron. In *Neanastatus*, the acropleuron is so large that it extends between the meso- and metacoxae, completely separating the metapleuron from the mesocoxa (Fig. 22). The metapleuron is bare (Fig. 18: pl_3) and its ventral and posterior margins are reflexed into translucent flanges along the acropleuron and base of the metacoxa, respectively.

Finally, *Eopelma* differs from other extant Neanastatinae in its comparatively short mesotarsi (cf. Figs 8, 10). The dorsal length of the basitarsus is only about three times the width of the segment and the middle three segments are angled so as to be higher



Figures 23–26. *Eopelma* sp. (♂): **23** dorsal head (Borneo) **24** lateral mesosoma (Borneo) **25** apex of acropleuron and metapleuron (Nepal) **26** apex of mesosternum and mesocoxae (Borneo).

than long. Consequently, the three middle segments have an oblique row of pegs along their anterior ventral margins (Figs 8, 10), although the longer basitarsus is similar to other Neanastatinae in having a row of pegs that continue distally along the apical margin of the segment (cf. Figs 8–10). Furthermore, at least the apical seta on the posterior ventral margin of the four basal mesotarsal segments is conspicuously long and spine-like in *Eopelma* (Fig. 10: psp), and sometimes more of the setae along the posterior ventral margin are somewhat spine-like. This peg pattern does not seem to be the same as that of some species of *Metapelma* and *Neanastatus* which have a variably developed double row of spines along the anterior ventral margin of at least the basitarsus. Some species of *Lambdobregma* also have a second inner row of somewhat stronger spine-like setae along the anterior ventral margin of the mesotarsus, but these are not conspicuously peg-like. Gibson (1989) also stated that *Eopelma* lacks mesotibial apical pegs, but there is a single, thicker, spine-like seta near the anteroapical margin of the tibia between the basitarsus and mesotibial spur that probably represents a single peg (Figs 8, 10: map?). Other extant Neanastatinae have a row of distinctly differentiated, dark, spine-like pegs along the anteroapical margin of the mesotibia (Fig. 9: map; see also figs in Gibson 1989). Gibson (1989) noted that the metatibia of *Lambdobregma* was moderately to distinctly compressed, but failed to mention that the exterior apical margin has 1 (species with subdivided scrobal channel) or 3 (species with undivided scrobal channel) short black pegs adjacent to the outer tibial spur that closely resemble mesotibial apical pegs. There often are stronger spines apically exterior to the outer metatibial spur in other Neanastatinae, but these do not closely resemble mesotibial apical pegs as in *Lambdobregma*.

Key to Genera of Neanastatinae

1 Acropleuron differentiated by uniformly developed crenulate sulcus curved to anterodorsal margin of pleuron near apex of prepectus (Figs 51, 60: acs); pronotum strongly transverse in dorsal view (Figs 49, 59: no_1) and almost vertical in lateral view (Figs 51, 60: no_1) [extinct] **2**

– Acropleuron differentiated by linear sulcus extended anteriorly to level at least in line with apex of tegula where obliterate (Figs 22, 24: acs) or extended dorsally as less distinct, posteriorly curved furrow or line to anterodorsal margin of pleuron near middle of prepectus (Fig. 41: acs); pronotum elongate-subtriangular in dorsal view (Figs 1–4, 27, 39: no_1) and with extensive dorsal surface in lateral view (Figs 19, 21) [extinct or extant] **3**

2(1) Head with occipital carina (Fig. 59: oc); axillae distinguished from scutellum by linear scutoscutellar sutures (Fig. 59: sss) and with inner angles separated by distance equal to about half own width; scutellum not carinate laterally (Fig. 59); fore wing with bare band separated from parastigma by setal region about equal in width to bare band (Fig. 62: spc); mesoscutum undifferentiated, lacking parapsidal ridges (Fig. 59) ..... ***Neanaperiallus* gen. n.**

– Head without occipital carina; axillae distinguished from scutellum by crenulate scutoscutellar sutures (Fig. 49: sss) and with contiguous inner angles; scutellum with carina extending along side from apex of axilla (Fig. 49: scc); fore wing with bare band contiguous with parastigma (Fig. 50: spc); mesoscutum differentiated into median and lateral regions by longitudinal, posteriorly ridged parapsidal lines (Figs 49, 51: psr) ..... ***Aspidopleura*** **gen. n.**

3(1) Scutellum divided mediolongitudinally (Figs 4, 17, 18); axillae with inner angles separated by at least twice own width (Figs 4, 17); head lenticular with vertex and temples carinately margined relative to occiput; fore wing with linea calva extending to base of wing along anal margin (Fig. 7: lc); flagellum with basal segment ring-like and with 5 distinct funicular segments .... ***Neanastatus*** **Girault**

– Scutellum undivided (Figs 1–3); axillae with inner angles contiguous (Figs 2, 3, 13, 15) or at most separated by distance about equal to own width (Figs 1, 11); head ovoid with vertex and temples smoothly rounded into occiput or only vertex carinately margined (Fig. 23); fore wing either entirely setose or with linea calva (Fig. 6: lc) extending only to basal cell; flagellum with or without differentiated ring segment, but with 7 or 8 distinct funicular segments **4**

4(3) Head and mesosoma patterned and at least partly yellowish to brown even if with some metallic luster (Fig. 1); scutellar-axillar complex with slightly divergent longitudinal grooves differentiating broadly separated quadrangular axillae on either side of anteriorly truncate scutellum (Figs 1, 11, 12); metanotum, propodeum and petiole all large and conspicuous regions posterior to scutellum (Figs 1, 11, 12); flagellum with 7 funicular segments..... ..... ***Eopelma*** **Gibson**

– Head and mesosoma uniformly dark with variably distinct metallic luster (Figs 2, 3); scutellar-axillar complex with strongly divergent grooves differentiating triangular axillae on either side of anteriorly angulate scutellum (Figs 2, 3, 13, 15, 40); metanotum medially concealed or overlain by apex of scutellum and petiole an inconspicuous, almost linear transverse strip (Figs 14, 15: ptl); flagellum with 8 funicular segments **5**

5(4) Acropleuron separated from metapleuron by convex, deeply divided upper and lower mesepimeron (Fig. 20: uep, lep); scutellum with carina extending along side from apex of axilla (Figs 2, 14: scc); metanotum with dorsellum V-like protuberant under scutellar apex (Figs 13: dor, 14) ..... ***Metapelma*** **Westwood**

– Acropleuron extending completely to metapleuron (Figs 21, 41); scutellum without carina along side (Figs 3, 15, 39); metanotum with dorsellum transverse under apex of scutellum (Figs 15, 16, 40)..... **6**

6(5) Mesoscutum with longitudinal parapsidal ridges differentiating elongate-rectangular median mesoscutal region from lateral regions (Fig. 39: psr); mesosternum without transepisternal sulcus (Fig. 41); hypopygium of female extending about half length of gaster (Fig. 35: hyp) [extinct] ..... ***Brevivulva*** **gen. n.**

– Mesoscutum not differentiated by ridged parapsidal lines (Figs 3, 21); mesosternum with transepisternal sulcus (cf. Figs 24, 26: tss); hypopygium of female extending almost to apex of gaster [extant] .....***Lambdobregma* Gibson**

Metapelma Westwood

Metapelma Westwood, 1835: 69. Type species: *M. spectabile* Westwood. By monotypy.
Halidea Förster, 1856: 31. Type species: *H. nobilis* Förster. Subsequent designation by Bouček (1988b: 547) (see Gibson 1989: 82); synonymy by Ashmead (1896: 5).
Halidayella Dalla Torre, 1897: 281. Unjustified emendation of *Halidea* Förster.

Metapelma archetypon Gibson, sp. n.

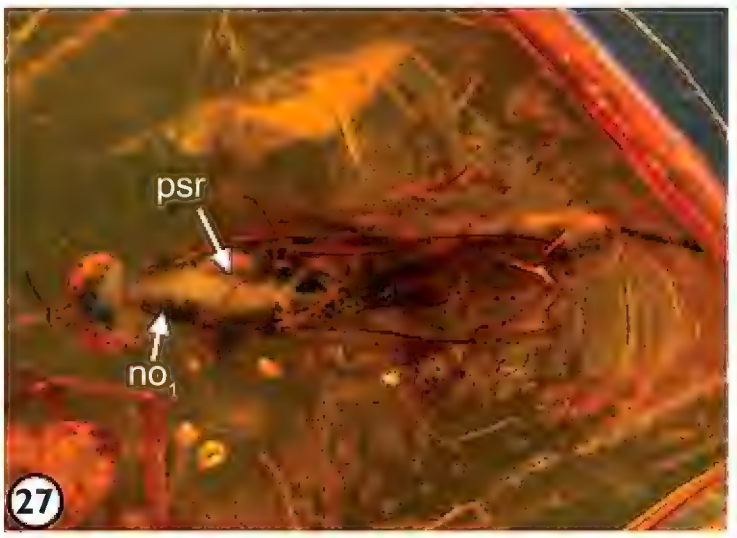
urn:lsid:zoobank.org:act:483192C9-E523-4884-84D0-99A5F82C6A75
Figs 27–32

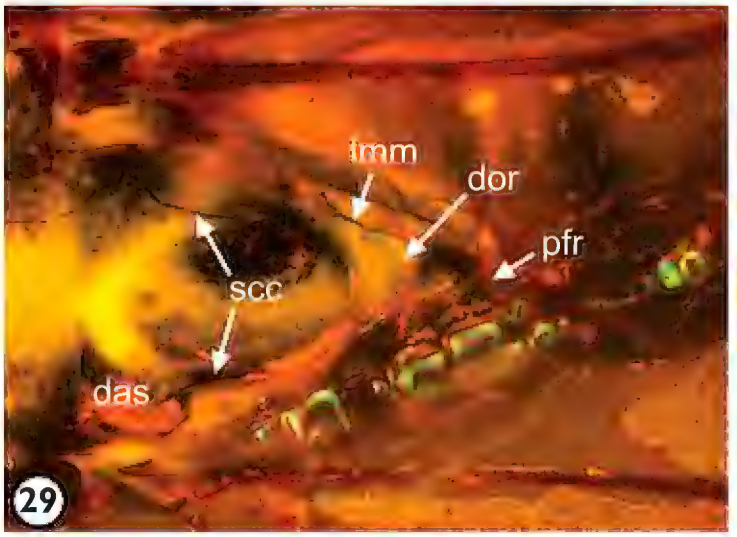
Etymology. The Greek word *archetypon*, meaning "original" or "model", in reference to the hypothesis that the head and hind leg structures represent uniquely retained groundplan states of the genus.

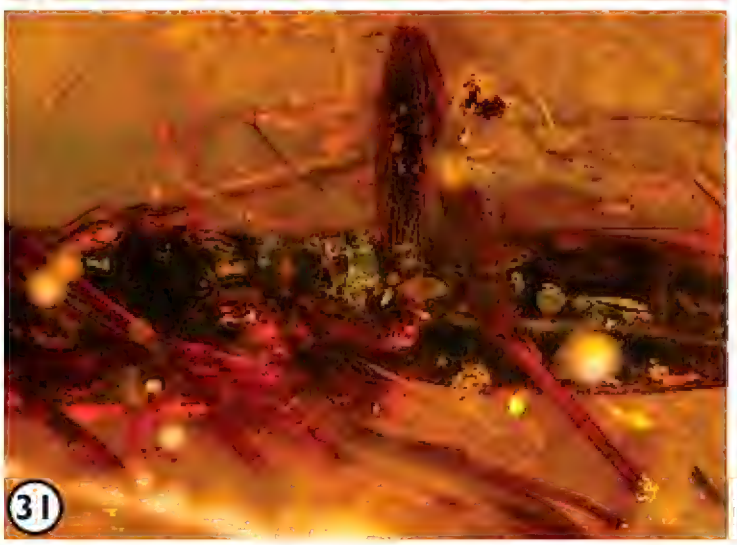
Type material. Holotype (Fig. 27): ♀, AMNH, labelled "AMNH BaJWJ-407" / "HOLOTYPE *Metapelma archetypon* Gibson". The unique female, along with partial remains of a spider, is in an almost rectangular, flat piece of Baltic amber about 13 × 11 × 3 mm. It is readily visible only from dorsal and ventral views and a white milky substance partly obscures dorsal mesosomal structure and gastral structure apically. Dorsal gastral structure is also partly hidden by the fore wings. Missing structures are left antenna beyond pedicel, right antenna beyond second funicular segment, right fore leg beyond about basal third of femur, right middle leg beyond tibia, left middle leg beyond part of basitarsal segment, and apical portion of ovipositor sheaths. The apical three segments of both hind tarsi are detached but are in the amber block.

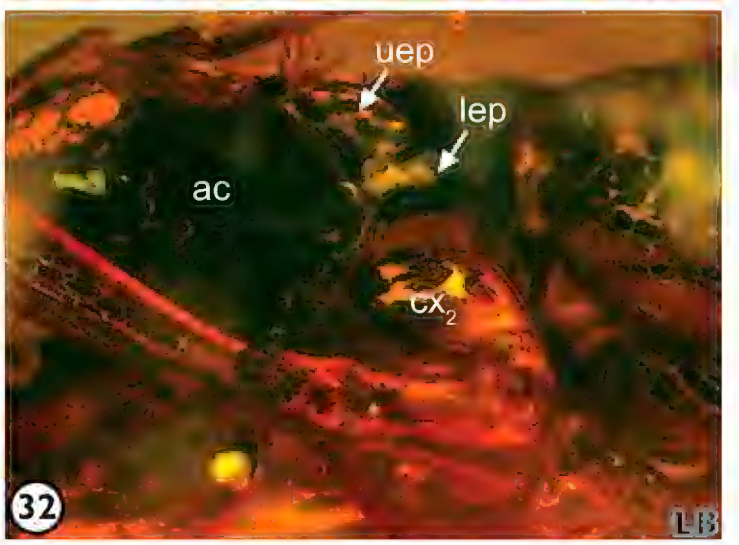
Description. Length = 7.7 mm, excluding ovipositor. Body uniformly dark except at least metatarsus yellowish. Head not visible in frontal view, but with quite high and narrowly convex interantennal region (Fig. 28: iar) separating distinct scrobes from low convex parascrobal regions in ventral or dorsal view, and in dorsal view with combined scrobal depression shallowed dorsally and smoothly merged with frons below ocelli. Head in lateral view ovoid; length of gena ventrally posterior to eye about two-thirds length of malar space; ventral margin of torulus about midway between lower occular line and oral margin. Head in dorsal view (Fig. 28) with vertex and temple rounded into occiput; transverse-rectangular, only about 1.7× as wide as long, with distinct temple about 0.25× head length; distance between eyes about 0.3× head width; posterior ocellus diameter equal to OOL and about 0.5× POL and 0.7× LOL; setal pattern not distinct but vertex, temples and occiput with white papilliform processes likely indicating setae surrounded by air pocket; occiput without occipital carina. Eye

superficially bare (Fig. 28), but dorsal part of left eye with white, papilliform processes similar to head dorsally and indicating eye probably densely microsetose. Antenna with scape elongate, compressed-ovoid, and widened distally; funicle with fu_1 about 2.9× as long as wide, about 0.7× length of fu_2 and 0.75× length of pedicel. Pronotum in dorsal view about 0.5× length of mesoscutum, sides anteriorly convergent and posterior margin incurved (Fig. 27: no_1); apparently uniformly setose similar to mesoscutum. Tegula elongate-triangular with almost truncate posterior margin. Mesoscutum (Fig. 27) not shoulder-like posterior to pronotum, slightly longer than greatest width; largely









Figures 27–32. *Metapelma archetypon* sp. n. (♀ holotype): **27** dorsal habitus **28** dorsal head **29** scutellar-axillar complex **30** fore wings **31** lateral mesosoma, gaster and hind leg **32** apex of acropleuron to base of gaster, ventrolateral view.

obscured by milky substance but apparently with posteriorly ridge-like parapsidal lines (Fig. 27: psr) differentiating slightly concave, elongate rectangular median region from inclined lateral regions; uniformly and quite densely setose. Scutellar-axillar complex (Fig. 29) with deep, longitudinally crenulate scutoscutellar sutures differentiating conspicuously convex scutellum and axillae, and entirely setose except with narrow median bare band over about apical two-thirds of scutellum; axillae with dorsal surfaces (Fig. 29: das) transverse-triangular and apparently with contiguous inner angles; scutellum with strong longitudinal carina (Fig. 29: scc) extending along side from near middle of inclined posterior surface of axilla. Metanotum concealed by milky white substance except for left panel lateral to dorsellum; panel wide laterally and narrowed medially toward apparently somewhat concave and posteriorly protuberant dorsellum (Fig. 29: dor) beneath and well separated from scutellar apex. Propodeum concealed by milky white substance except for left side, apparently without differentiated plical and callar regions but depressed anteromedially under dorsellum and with posterior margin (foramen) shallowly incurved (Fig. 29: pfr); spiracle near midlength laterally. Prepectus triangular, about as long as high with dorsal and ventral margins forming obtuse posterior angle (cf. Fig. 19). Mesopleuron with acropleuron (Fig. 32: ac) extending slightly posterior of level of anterior margin of mesocoxa (Fig. 32: cx_2), with linear acropleural sulcus extending anteroventrally from mesocoxa for at least about one-third length before obliterate; mesepimeron a convex, arcuate-subtriangular region above base of mesocoxa, the region subdivided by deep sulcus into quadrangular lower mesepimeron (Fig. 32: lep) comprising about ventral third and triangular upper mesepimeron (Fig. 32: uep) comprising about dorsal two-thirds. Metapleuron entirely setose, more or less triangular in lateral view but ventral margin narrowly truncate above base of mesocoxa between mesepimeron and metacoxa. Mesosternum largely concealed, but with sulcate discrimen. Presence or absence of protibial apical spicule not visible. Middle legs long; mesocoxa with large basolateral cavity (cavity faced anteriorly because only visible mesocoxa twisted and slightly rotated out of fossa, Fig. 32); presence or absence of mesotibial pegs not visible, but tibial spur about 3× as long as apical width. Hind leg (Fig. 31) with metatibia 9× as long as maximum width, slightly narrower than femur with dorsal and ventral margins subparallel over most of length, and compressed-oval in cross section, dorsal margin apparently angulate but not carinate or thin; metatarsus with segments compressed-cylindrical, subequal in width and without carinate dorsal margin; basitarsus about 8x as long as wide. Fore wing (Fig. 30) hyaline; costal cell extensively setose along leading margin, but bare along submarginal vein; basal cell and disc completely setose except for very narrow linea calva not quite extending to basal fold; cubital and vannal areas bare except for some setae along posterior margin of vannal area distally; cc: mv: pmv: stv = 5.5: 1.8: 4.0: 0.9; stigmal vein with distinct uncus. Gaster very broadly sessile, elongate-fusiform, with at least 7 setose gastral tergites (structure of distal tergites not clearly visible, but apparently with deep suture lateral to cercus subdividing apical tergite and with Gt_6 extending dorsally over most of subdivided region); without projecting anal filament; hypopygium extending about 0.85× length of gaster. Ovipositor sheaths projecting, slender and obviously elongate, but apices missing.

Biology. Unknown, but likely the species was a parasitoid of wood-boring beetles based on structure of its ovipositor sheaths (Fig. 27) and hypothesized relationships with other species of *Metapelma*.

Remarks. Because of its preservation several important features cannot be seen clearly in the unique female of *M. archetypon* though it does appear to have posteriorly ridged parapsidal lines (Fig. 27: psr) and relative dimensions of its metanotum and propodeum are at least similar to extant *Metapelma* (cf. Figs 2, 29). Most features that are clearly visible, such as the scutellar-axillar complex, acropleural sulcus, pronotum, tegula, and fore wings are very similar to extant *Metapelma*. Phylogenetically most significant is that *M. archetypon* has a deeply divided upper and lower mesepimeron separating the acropleuron and metapleuron (Fig. 32), which is unique to *Metapelma* (Figs 19, 20) (Gibson 1989, character 3, state 2). It differs conspicuously from extant *Metapelma* by having normal hind legs (Fig. 31). Extant species are uniquely characterized by laminately compressed metatibiae and metatarsi, and the metatarsal segments being obviously narrowed distally. The head of *M. archetypon* also appears to be more ovoid in lateral view than for extant species, having a comparatively long vertex and temples as well as a much more highly convex interantennal region (Fig. 28: iar) and longer, deeper scrobes. This latter structure is similar to what Gibson (1989, character 3, state 1) hypothesized as the ground plan structure for Neanastatinae and indicates that the somewhat lenticular head and short, furrow-like scrobes of extant *Metapelma* (Gibson 1989, fig. 14) evolved convergently to the similar head structure of *Neanastatus* (Gibson 1989, fig. 13) rather than being a synapomorphy for the two genera. Based on the above hypotheses of character-state transformation and relationships I hypothesize that *M. archetypon* is the sister species of all extant *Metapelma* and prefer to expand the generic limits of *Metapelma* to include it rather than to establish a new genus.

***Brevivulva* Gibson, gen. n.**
urn:lsid:zoobank.org:act:5998648E-2E18-454B-B17E-B921EC1FF261
Type species: *Brevivulva electroma* sp. n.

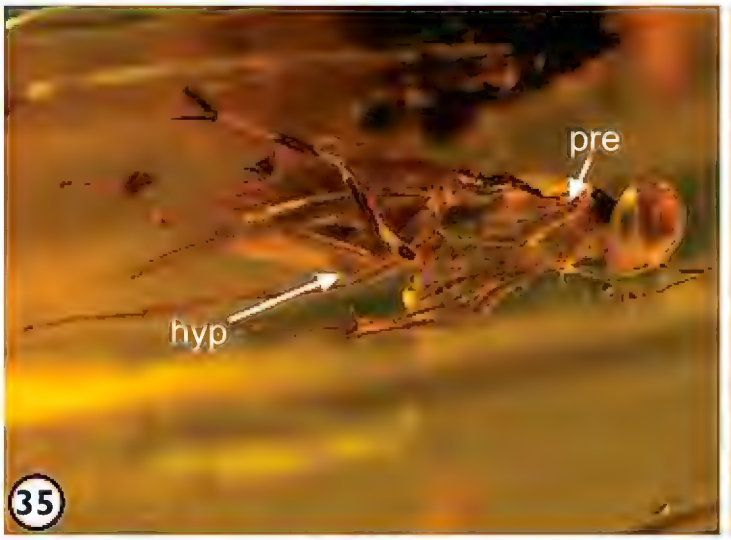
***Brevivulva electroma* Gibson, sp. n.**
urn:lsid:zoobank.org:act:594F760F-5932-4157-BDA2-1D5CE50E1500
Figs 33–44

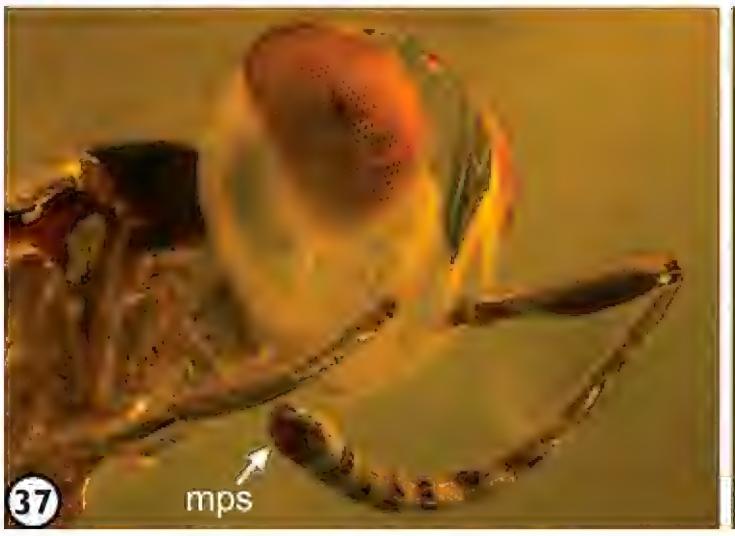
Etymology. The generic name is formed from the Latin words *brevis*, meaning "short", and *vulva*, meaning "cover" or "wrapper", in reference to the short hypopygium compared to *Lambdobregma*. The species name is formed from the Latin word *electrum*, meaning "amber".

Type material. Holotype (Figs 33–35): ♀, AMNH, labelled "AMNH BaJWJ-408" / "HOLOTYPE *Brevivulva electroma* Gibson". The unique female is near one end of a piece of Baltic amber that is triangular in cross section and about 21 mm long and 5

mm wide when it is faced dorsally. The specimen is complete but a white milky substance obscures the right half of the lower face and mouthparts (Figs 37, 38), and the ventral surface of the gaster beyond the hypopygium (Fig. 34).

Description. Length = 3.25 mm, including ovipositor sheaths. Body dark with faint metallic green luster on mesosoma under some angles of light. Head in frontolateral view (Fig. 37) with convex interantennal region separating ventrally distinct scrobes, dorsally continuous scrobal depression shallowed dorsally and smoothly merged with frons below ocelli; face uniformly coriaceous and setose except scrobes bare; parascrobal region incurved slightly and ridged from beside torulus to level about equal with dorsal angle of interantennal region (Fig. 38). Head in lateral view with

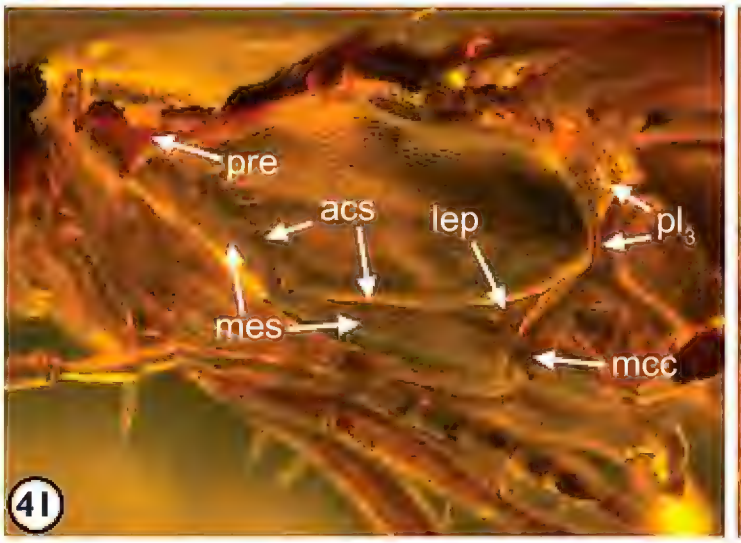


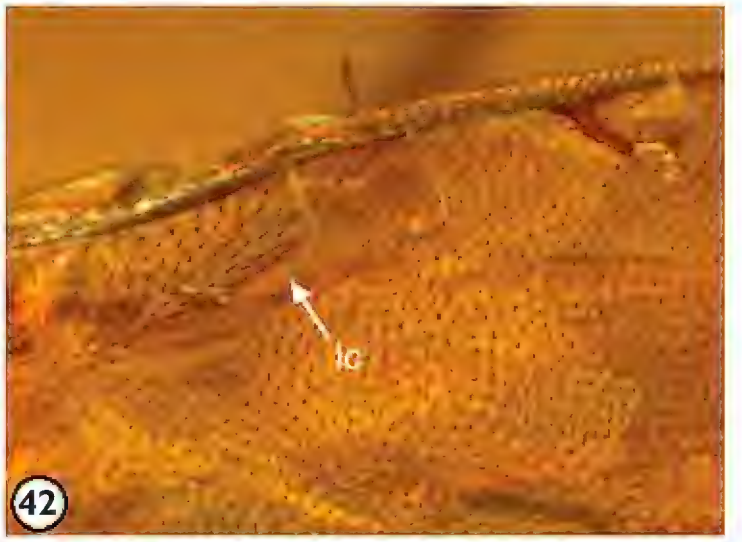


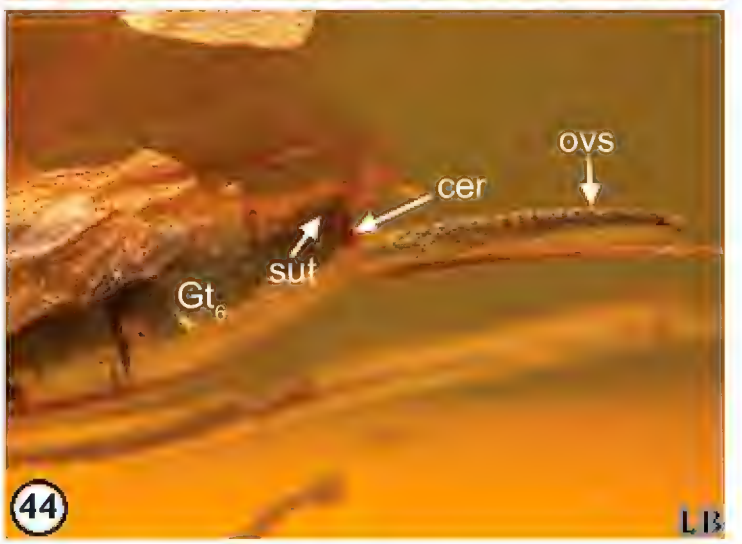
Figures 33–38. *Brevivulva electroma* sp. n. (♀ holotype): **33** dorsal habitus **34** ventral habitus **35** ventrolateral habitus **36** dorsal head **37** frontolateral head **38** frontal head.

length of gena posterior to eye subequal to malar space. Head in dorsal view (Fig. 36) with vertex and temple rounded into occiput; about 1.6× as wide as long; distance between eyes about 0.3× head width; maximum diameter of ovoid posterior ocellus about 2.5× OOL and 0.5× POL; occiput without occipital carina. Eye at least superficially bare (Figs 36–38). Antenna (Figs 37, 38) 13-segmented with ratio of segments = 12.5: 5.2: 2.2: 4.5: 3.2: 3.2: 3.2: 3.0: 2.8: 2.6: 5.2; scape narrow and cylindrical basally, but about apical two-thirds widened; funicle with 8 segments, fu_1 about 1.5× longer than wide, fu_2 the longest segment and subsequent funicular segments increasingly shorter and wider; clava compact 3-segmented with sutures almost straight transverse and with only small micropilose sensory region ventroapically (Fig. 37: mps). Pronotum in dorsal view (Figs 33, 39: no_1) about half length of mesoscutum, sides anteriorly convergent and posterior dorsal margin slightly incurved; dorsal surface slightly convex, finely mesh-like coriaceous-reticulate. Tegula elongate-triangular with almost truncate posterior margin. Mesoscutum (Fig. 39) not shoulder-like posterior to pronotum, as long as greatest width, and with posteriorly ridge-like, parallel parapsidal lines (Fig. 39: psr) differentiating slightly concave, elongate-rectangular median region from inclined lateral regions; sparsely and inconspicuously setose; median mesoscutal region with larger and more distinct mesh-like reticulation than on pronotum, lateral mesoscutal regions with sculpture similar to median region but apparently shallower, more coriaceous toward lateral margin, and parapsidal lines with much smaller and finer coriaceous sculpture. Scutellar-axillar complex with distinct, longitudinally crenulate scutoscutellar sutures (Figs 39, 40: sss) differentiating convex axillae and scutellum; axillae equilateral-triangular with contiguous inner angles, with finer coriaceous sculpture compared to mesoscutum, and without distinct setae; scutellum not laterally carinate, coriaceous-imbricate anteriorly to meshlike-reticulate posteriorly and apparently quite uniformly and sparsely setose, protuberant posteromedially, the protuberance (Fig. 40: scp) projecting ventrally into medial depression of metanotum. Metanotum (Figs 39, 40: no_3) strongly transverse, slender, with posterior margin almost straight-transverse and with anterior margin U-like reflexed under scutellar protuberance so as to apparently form concave, cup-like region having a vertical posterior surface. Propodeum in dorsal view (Figs 40, 41) very short; plical region strongly transverse with shallowly incurved foramen (Fig. 40: pfr) and apparently slightly concave medially under scutellar-metanotal protuberance; spiracle near midlength laterally. Prepectus (Figs 35, 41: pre) conspicuously elongate-triangular, the apical half abruptly narrowed and tapered to acute angle. Mesopleuron (Fig. 41) with uniformly convex acropleuron extending posteriorly to region between bases of meso- and metacoxae, with linear acropleural sulcus (Fig. 41: acs) extending forward from mesocoxa to level about equal with base of tegula where abruptly recurved dorsally as obscure arcuate line extending to prepectus near apical third; acropleuron bare, mesh-like reticulate anteriorly to more finely coriaceous posteriorly, the sculpture elongated and more or less aligned in rows posteriorly; mesepisternum sparsely setose anterior to arcuate portion of acropleural sulcus and ventral to horizontal portion of sulcus (Fig. 41: mes) except for bare, triangular remnant of mesepimeron (Fig. 41: lep) between acropleuron and mesosternum.

Metapleuron uniformly setose, strongly tapered ventrally so as to extend as almost linear strip (Fig. 41: pl_3) between acropleuron and metacoxa to base of mesocoxa. Mesosternum (Fig. 34) with deep sulcate discrimen, without transepisternal sulcus, and with straight-transverse posterior margin abutting mesocoxae. Protibia apparently with apical spicule. Middle leg conspicuously long (Figs 33–35), about as long as body and longer than hind leg; mesocoxa with large basolateral cavity opposite angle formed between acropleuron and mesepisternum (Fig. 41: mcc); mesotibia with row of dark, variably long spines along apical margin (Fig. 43: map) and with mesotibial spur about 3x as long as apical width of tibia; mesotarsus (Fig.43) slender with subcylindrical seg-







Figures 39–44. *Brevivulva electroma* sp. n. (♀ holotype): **39** dorsal mesosoma **40** scutellar axillar complex to base of gaster **41** mesosoma, ventrolateral view **42** middle part of fore wing **43** mesotarsus and tibial spur **44** posterior of gaster, lateral view.

ments, the basal four segments with even row of short pegs along at least anterior ventral margin and apical peg on slightly higher plane than others (i.e., also on apical margin of respective segment). Hind leg with tibia and tarsus slender, subcylindrical, and apparently without black, peg-like spines along apical margin exterior to outer spur. Fore wing hyaline (Figs 33, 42); costal cell extensively setose along leading margin; basal cell and disc uniformly setose except for linea calva (Fig. 42: lc) behind parastigma, anterior margin of bare band delimited by slightly thicker microtrichia; cubital and vannal areas apparently bare; cc: mv: pmv: stv = 5.5: 2.7: 3.1: 0.9; stigmal vein with distinct uncus. Gaster very broadly sessile, with at least seven uniformly setose gastral tergites; cercus (Fig. 44: cer) at extreme posterior margin of terminal segment; terminal segment with transverse suture (Fig. 44: sut) anterior to cercus delimiting apparently fused Gt_7 and Gt_8, the presumptive Gt_8 comprising about apical quarter of syntergum and length of syntergum about 0.6× length of Gt_6; hypopygium extending about half length of gaster (Fig. 35: hyp). Ovipositor sheaths (Fig. 44: ovs) projecting by slightly less than half length of gaster, tapered and slightly curved down apically.

Biology. Unknown, but the exerted, stiff ovipositor sheaths suggest the species was a parasitoid of wood-boring beetles or other hosts in concealed situations.

Remarks. *Brevivulva electroma* closely resembles species classified in the extant genus *Lambdobregma*, including having a conspicuously elongate-triangular prepectus that narrows abruptly posteriorly (Figs 35, 41: pre; Gibson 1989, fig. 40). It keys readily to *Lambdobregma* using Gibson (1989) except for the absence of transepisternal sulci, but differs also by having posteriorly carinate, ridged parapsidal lines (Fig. 39: psr), the hypopygium extending only about half the length of the gaster (Fig. 35: hyp) rather than almost to its apex, Gt_6 not concealing the syntergum, and the cercus at the extreme posterior margin of the syntergum (Fig. 44: cer). It also differs in having what appear to be slightly less derived relative structures of two features. Species of *Lambdobregma* have a conspicuously elongate-slender acropleuron (Fig. 21) that extends to the base of the metacoxa so that in lateral view the acropleuron conceals the linear, bare, ventral extension of the metapleuron (Fig. 16), whereas in *B. electroma* a setose ventral strip of the metapleuron remains between the acropleuron and metacoxa (Fig. 41: pl_3) because the acropleuron is slightly less elongate. The scutellum is also posteromedially protuberant in both *B. electroma* and *Lambdobregma*, but in *Lambdobregma* it extends as a hook-like process over the metanotum into a depression of the propodeum (Figs 15, 16). In *B. electroma* the scutellar protrusion only extends into a medially concave portion of the metanotum (Fig. 40: scp, no_3). Head structure of *B. electroma* resembles that of the undescribed species of *Lambdobregma* from Chile because both have a Λ-shaped scrobal depression (Figs 37, 38), whereas other *Lambdobregma* have a subdivided scrobal depression (Gibson 1989, fig. 15). The Chilean species also lacks setae from the propodeal plical region similar to *B. electroma*, but apparent absence from *B. electroma* may be an artifact of preservation.

The features discussed above suggest *B. electroma* could be the sister species of the Chilean species + other extant *Lambdobregma*, but absence of parapsidal lines and relative scutellar-metanotal-propodeal structure could also support it as the sis-

ter group of *Lambdobregma* + *Neanastatus* (see Discussion). Because of the uncertain relationships of *B. electroma* and because it is differentiated from extant *Lambdobregma* by several features I prefer to establish a new genus for it rather than expanding the generic limits of *Lambdobregma*.

***Aspidopleura* Gibson, gen. n.**
urn:lsid:zoobank.org:act:A67807A6-2C25-48DE-B063-A1B1FDDBCE7A
Type species: *Aspidopleura baltica* sp. n.

***Aspidopleura baltica* Gibson, sp. n.**
urn:lsid:zoobank.org:act:5E2311CE-AB47-42CF-9A7B-37BEEDACEA3C
Figs 45–56

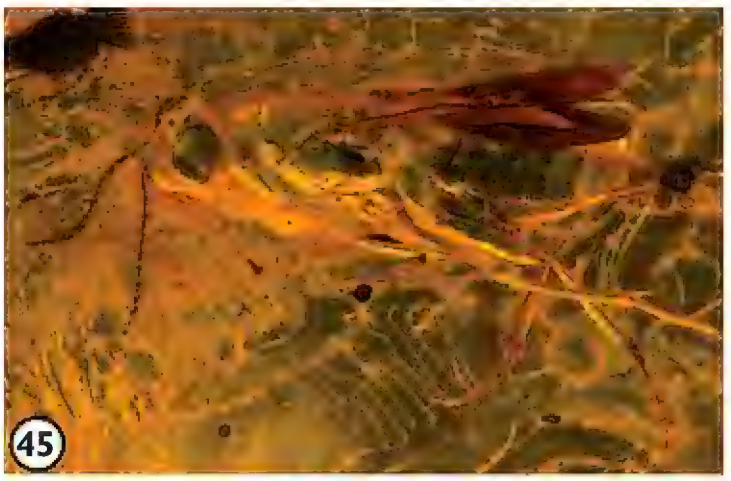
Etymology. The generic name is formed from the Greek words *aspido*, meaning "shield" and *pleuro*, meaning "side", in reference to its shield-like acropleuron. The species name is in reference to the amber origin.

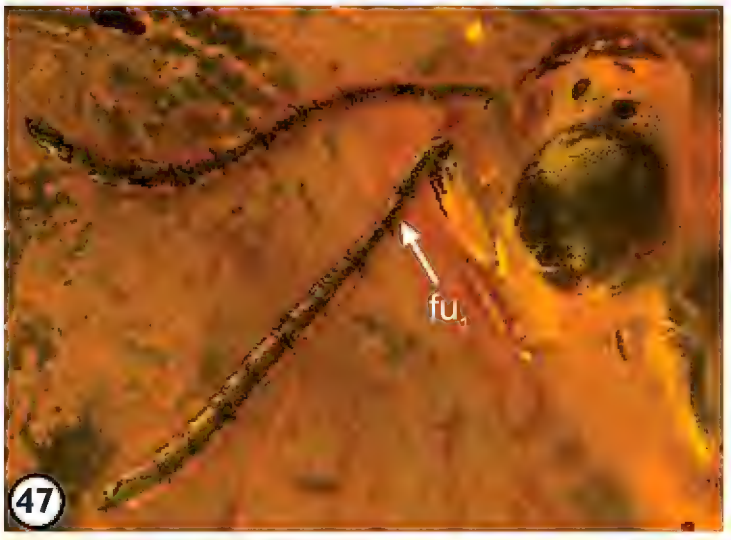
Type material. Holotype (Fig. 45): ♀, AMNH, labelled "AMNH-JWJ-409" / "HOLOTYPE *Aspidopleura baltica* Gibson". The holotype female is in a flat, spatulate piece of Baltic amber about 24 × 18 × 4 mm. The specimen is entire, but not visible from direct dorsal view and most of the right side is not visible because of an internal plane of irregularities (the right middle leg extends through the plane of irregularities) and with a crack extending from near the apex of gaster obscuring syntergal structure.

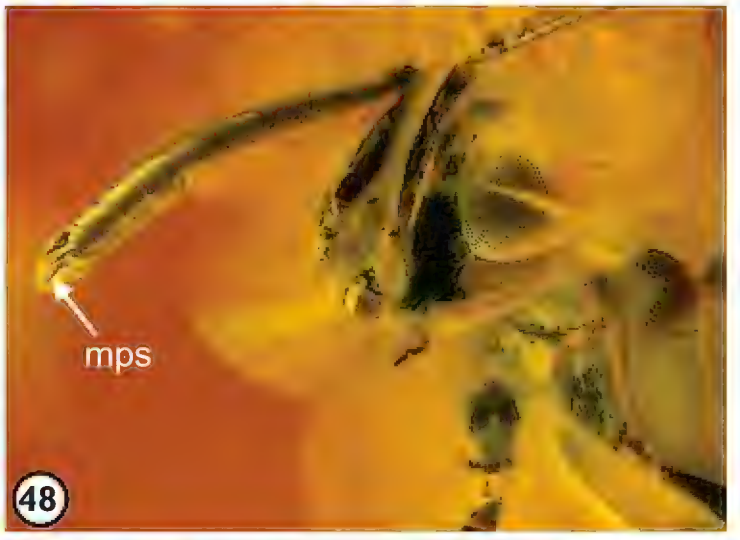
Paratype (Fig. 46): ♀, AMNH-JWJ-410. The paratype female is in a flat, triangular piece of Baltic amber about 19 × 14 × 6 mm. The specimen is entire, but its structure is partly obscured by pits in the surface of the amber block, a white milky substance around the specimen, and other internal artifacts.

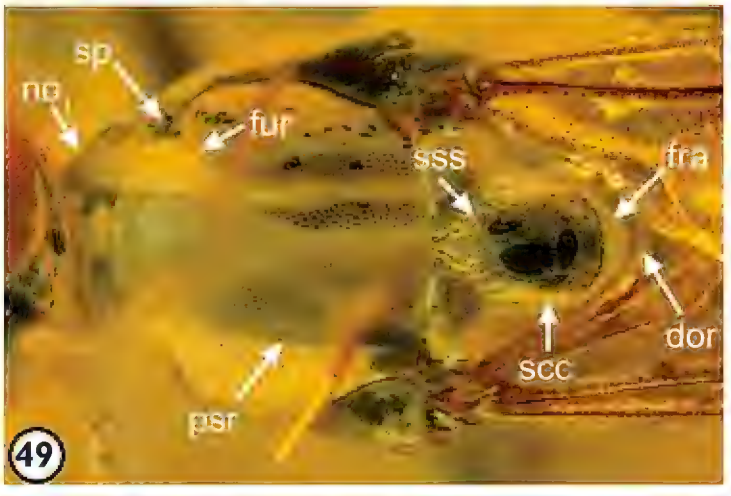
Description. Length = 4.2 mm, including ovipositor. Body uniformly dark brown. Head in frontolateral view (Fig. 48) with convex interantennal region separating ventrally distinct scrobes, dorsally continuous scrobal depression shallowed dorsally and smoothly merged with frons below ocelli; parascrobal region incurved slightly and almost carinately margined from beside torulus to level about equal with dorsal angle of interantennal region; torulus with dorsal margin about in line with lower ocular margin (Fig. 48) and distance between ventral margin and oral margin about equal to its height; face uniformly coriaceous and setose except scrobes bare; clypeus with apical margin straight transverse. Head in dorsal view with vertex and temple rounded into occiput (Figs 47, 49); distinctly transverse, but relative dimensions not measurable; maximum diameter of ovoid posterior ocellus about 3× OOL and about 0.75× LOL (POL ratio not measurable accurately); occiput without occipital carina. Eye at least superficially bare (Figs 46–48). Mandible with small ventral tooth and slightly concave dorsal truncation (Fig. 48), tooth segregated from dorsal truncation by groove extending toward mandibular base. Antenna (Figs 47, 48) 13-segmented, scape foreshortened but ratio of segments from pedicel = 2.0:

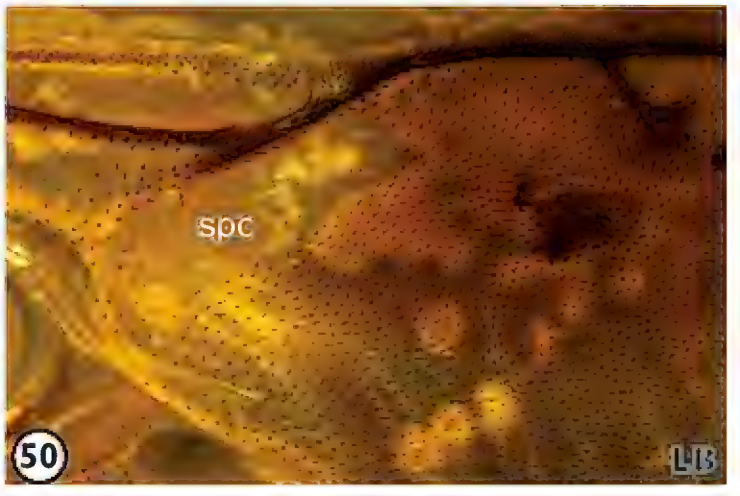
1.2: 1.6: 1.6: 1.5: 1.4: 1.2: 1.2: 1.1: 2.1; scape (Fig. 47) elongate-rectangular, inner surface flat and outer surface dorsally convex and ventrally thin, flange-like; funicle with 8 segments, fu_1 (Fig. 47: fu_1) almost twice as long as wide and all segments except apical segment longer than wide and increased slightly in width apically; clava compact 3-segmented with sutures strongly oblique in lateral view (Fig. 47, upper antenna) so in ventral view (Fig. 48) two basal segments very short and with micropilose sensory region on terminal segment forming ventral channel if collapsed (Fig. 48: mps). Pronotum in dorsal view about one-third length of mesoscutum (Fig. 49: no_1, anterior portion of pronotum concealed by head), setose, with surface sloping from posterior margin; in lateral view (Fig. 51: no_1) almost vertical with dorsal half







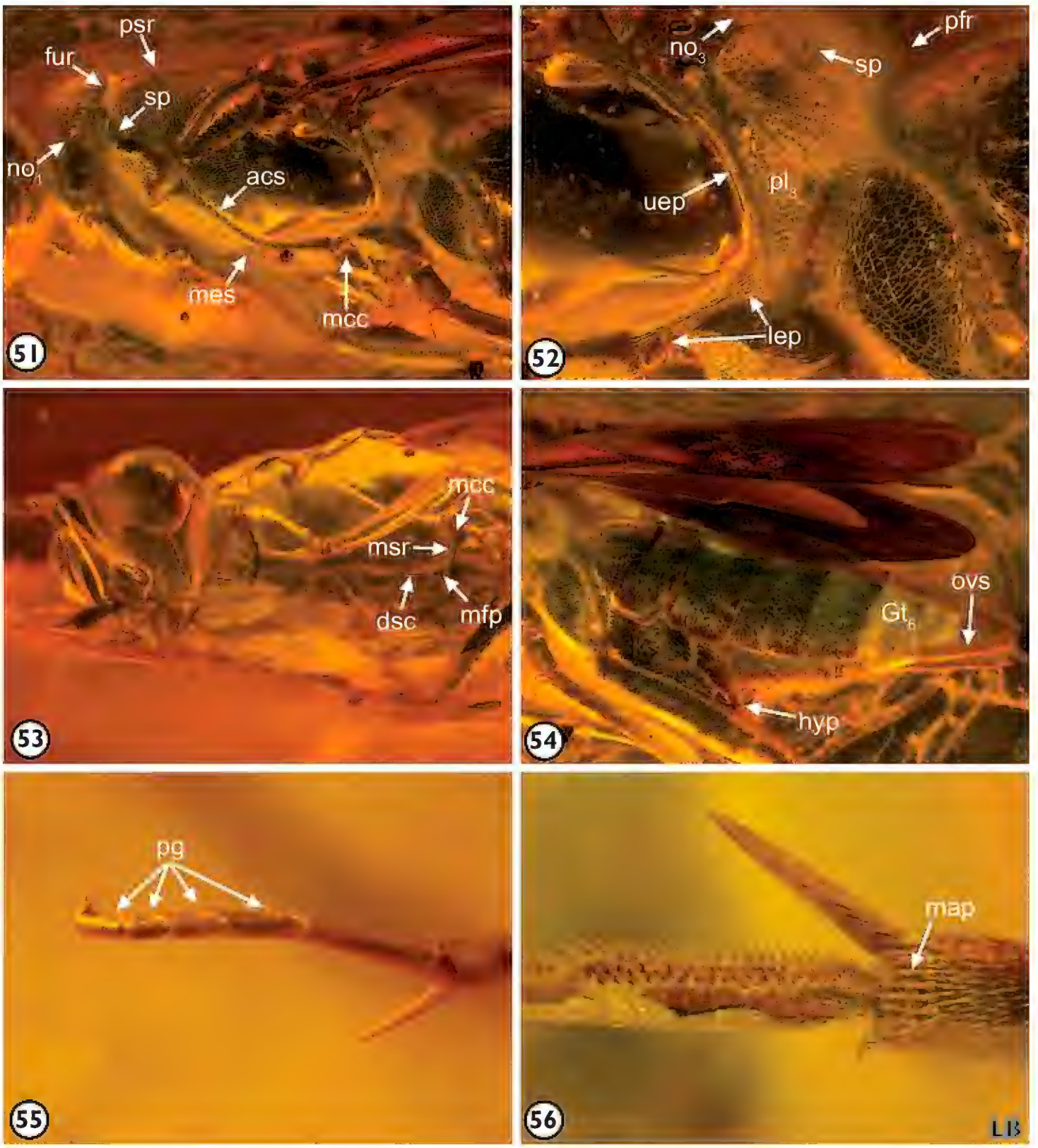




Figures 45–50. *Aspidopleura baltica* sp. n. (♀): **45** lateral habitus (holotype) **46** dorsal habitus (paratype) **47** dorsolateral head and antennae (holotype) **48** frontolateral head and antennae (paratype) **49** dorsal mesosoma (paratype) **50** middle part of fore wing (paratype).

only slightly convex. Tegula elongate-triangular with almost truncate posterior margin. Mesoscutum (Figs 46, 49) slightly shoulder-like posterior to pronotum, very slightly wider than long, and with parallel, posteriorly ridge-like parapsidal lines (Fig. 49: psr) differentiating median region from inclined lateral regions, median region slightly concave posteriorly but convex anteriorly where delineated laterally by shallow, convergent furrows (Figs 49, 51: fur) originating mesal to respective spiracle (Figs 49, 51: sp); uniformly setose; median mesoscutal region mesh-like reticulate, reticulations isodiametric anteriorly but more elongate posteromedially; parapsidal lines with much smaller and finer sculpture; lateral mesoscutal region with fine sculpture dorsally graduating to mesh-like sculpture ventrally (Fig. 51). Scutellar-axillar complex with distinct, longitudinally crenulate scutoscutellar sutures (Fig. 49: sss) differentiating convex axillae and scutellum; axillae equilateral-triangular with contiguous inner angles, sparsely setose and with much finer and smaller coriaceous sculpture compared to mesoscutum; scutellum with longitudinal carina along side extending from apex of axilla (Fig. 49: scc) and with frenum occupying about 0.15 median length differentiated by transverse, curved line (Fig. 49: fra), frenum bare, isodiametric-reticulate to coriaceous with evenly curved posterior margin, the margin not noticeably protuberant medially or ventrally but separated slightly from underlying metanotum, and scutellum anterior to frenum bare medially but otherwise sparsely, uniformly setose with setae not lengthened posteriorly, and mesh-like coriaceous with sculpture becoming more elongate laterally. Metanotum mostly concealed, but differentiated into lateral panels and dorsellum; dorsellum with convex posterior surface and flat dorsal surface extending from under scutellum slightly beyond apex (Fig. 49: dor). Propodeum mostly concealed but transverse and apparently without differentiated plical and callar regions except for sulcus extending from anterior margin to about level of posterior margin of spiracle adjacent to outer margin of spiracle; crenulate along anterior margin and broad, shallowly incurved foraminal margin (Fig. 52: pfr); spiracle (Fig. 52: sp) comparatively large, anterior margin separated from anterior margin of propodeum by distance about equal to its own diameter and posterior margin at about midlength of propodeum; callar region setose lateral to spiracle (Fig. 52). Prepectus (Figs 48, 51) equilateral triangular, about as long as high, with dorsal and ventral margins forming obtusely rounded posterior angle extending to base of tegula; mesh-like reticulate except much more finely coriaceous along dorsal and ventral margins. Mesopleuron with uniformly convex acropleuron extending virtually to metapleuron and base of mesocoxa, but acropleuron separated from mesocoxa by transverse, bare, strigose-punctulate lower mesepimeron (Fig. 52: lep) that extends dorsally as linear band between acropleuron and metapleuron (Fig. 52: uep); acropleuron differentiated by crenulate acropleural sulcus (Fig. 51: acs) directed straight forward from mesocoxa for about half length of mesopleuron where evenly curved dorsally to near apex of prepectus, bare, distinctly though finely mesh-like coriaceous anteriorly in angle between acropleural sulcus and tegula, but sculpture faded dorsally and posteriorly so as to be smooth and shiny below base of wings and over at least posterior third; mesepisternum setose ventral

to acropleural sulcus (Fig. 51: mes). Metapleuron (Fig. 52: pl_3) uniformly setose, triangular, with anterior and posterior margins converging ventrally and extending to base of mesocoxa between acropleuron/mesepimeron and metacoxa. Mesosternum with sulcate discrimen (Fig. 53: dsc), without transepisternal sulcus, and posterior to mesofurcal pit (Fig. 53: mfp) with slender marginal rim (Fig. 53: msr) abutting mesocoxae. Presence or absence of protibial spicule not visible. Middle leg not lengthened conspicuously, at most about as long as hind leg (Fig. 45); meso-



Figures 51–56. *Aspidopleura baltica* sp. n. (♀ holotype): **51** lateral mesosoma and base of gaster (holotype) **52** posterior third of mesosoma, lateral view (holotype) **53** ventrolateral head and ventral mesosoma **54** lateral gaster **55** mesotarsus and tibial spur, dorsal view **56** apex of mesotibia and basitarsus, lateral view.

coxa with large basolateral cavity opposite angle formed between acropleuron and mesepisternum (Figs 51, 53: mcc); mesotibia with two rows of distinctly differentiated, spine-like pegs apically (Fig. 56: map), and with mesotibial spur only about 1.5x as long as apical width of tibia; mesotarsus slender (Fig. 55), apparently with spine-like setae along posterior ventral margin and more peg-like spines along anterior ventral margin of at least basitarsus (Fig. 56), and with distinct peg distally on basal four segments (Fig. 55: pg). Hind leg with tibia and tarsus slender. Fore wing with large brownish region behind marginal and postmarginal veins, color fading distally and not extending over speculum (Fig. 46); costal cell bare except narrowly setose along leading margin; basal cell broadly bare along submarginal vein except apically; disc uniformly setose except for elongate-rectangular speculum contiguous with parastigma and basal fold to cubital fold (Fig. 50: spc); cubital and vannal areas bare; basal fold pigmented apically, forming spur of parastigma (Fig. 50); cc: mv: pmv: stv = 5.5: 2.7: 3.0: 1.3; stigmal vein apically curved into distinct uncus. Gaster (Fig. 54) very broadly sessile, with seven uniformly setose and coriaceous-aciculate gastral tergites; structure of syntergum not clearly visible, but apparently shorter than Gt_6; hypopygium extending about half length of gaster (Fig. 54: hyp) Ovipositor sheaths (Fig. 54: ovs) projecting, but by distance only about equal to length of basitarsus of middle leg.

Biology. Unknown, but the short ovipositor sheaths and bidentate mandibular structure similar to typical members of *Anastatus* Motschulsky (Eupelminae) might indicate the species was an egg parasitoid.

Remarks. Unlike the previous two described taxa, *A. baltica* does not closely resemble species of any extant neanastatine genus. It is uniquely distinguished by a large fore wing speculum (Fig. 50: spc) that extends to the cubital fold and is contiguous with the parastigma and basal fold. It is also the only neanastatine to have a distinct frenum (Fig. 49: fra), though the transverse apical scutellar region of *Eopelma* (Figs 11, 12: smr) and the much less conspicuous scutellar rims of other extant Neanastatinae (Figs 14, 16, 18: smr) may represent secondary modifications that are homologous with a frenum. Its pronotal-mesoscutal structure is also unusual because the mesonotum is slightly shoulder-like posterior to a dorsally transverse pronotum and the mesoscutum is convex anteriorly and shallowly concave posteriorly between convex lateral lobes (Fig. 49). This structure more closely resembles typical winged female Eupelminae (see figs in Gibson 1995) than other Neanastatinae and is a consequence of the almost vertical pronotum of *A. baltica* not extending posteriorly over the anterior part of the mesoscutum as much as in extant Neanastatinae, which have longer pronota (Figs 1–4, 27, 33). I am uncertain of the mesotarsal peg pattern of *A. baltica*. The mesotarsus at least has stronger spines forming a more or less double row along its anterior ventral margin (Fig. 56) similar to some *Metapelma* and *Neanastatus*. The most apical spine of each segment may also be on a higher plane on the anteroapical margin of the respective segment because they are seen from a somewhat dorsal view (Fig. 55: pg) and, if so, the mesotarsal peg pattern of *A. baltica* is similar to the pattern that characterizes extant Neanastatinae (Figs 8–10).

***Neanaperiallus* Gibson, gen. n.**
urn:lsid:zoobank.org:act:6654E412-1382-46E9-BDE1-3BDA2469B95C
Type species: *Neanaperiallus masneri* sp. n.

***Neanaperiallus masneri* Gibson, sp. n.**
urn:lsid:zoobank.org:act:EC851A80-6D5A-40CA-B8E3-643416DA99F2
Figs 57–65

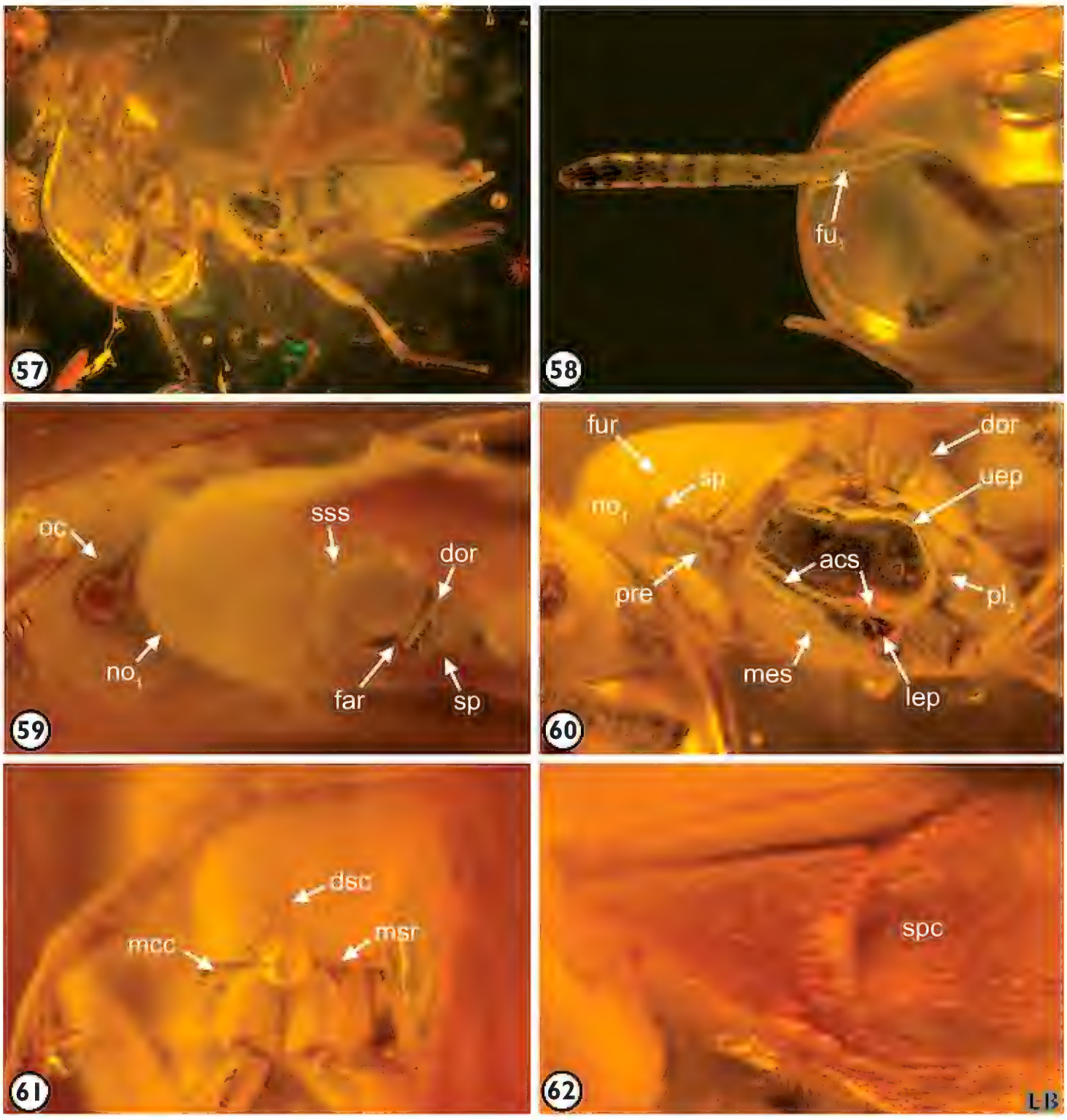
Etymology. The genus name is formed from the first part of the subfamily name, Neanastatinae, and the Greek word *periallos*, meaning "before all others", in reference to the postulated relationships of this genus to other genera classified in the subfamily. The species name is in honour of Dr. Lubomír Masner, who also is "before all others" in his enthusiasm for entomology and life, his unparalleled efforts in collection development, and his contributions to the systematics and understanding of parasitic wasps.

Type material. Holotype (Fig. 57): ♀, AMNH, labelled "BALTIC AMBER: Eocene (Lutetian), purchased (2007) from Jens-Wilhelm Janzen AMNH B-JWJ-265" / "HOLOTYPE *Neanaperiallus masneri* Gibson". The unique female is in a flat piece of Baltic amber having a circumference formed of five sides of different lengths. The specimen is entire, but its right side is completely obscured by a white milky substance, a large bubble obscures most of the frontal surface of its head (Figs 57, 58), the right wings obscure most of metanotum, propodeum and gaster dorsally, and minute air bubbles reduce clarity of observation.

Description. Length = 3.3 mm including ovipositor sheaths. Body superficially yellow, but probably uniformly brown based on acropleuron and part of first two gastral tergites. Head in dorsolateral view ovoid with vertex and temple rounded into occiput; dimensions not measurable but certainly wider than high and torulus apparently conspicuously below lower occular line; occiput with ∩-shaped occipital carina (Fig. 59: oc); face not clearly visible, but apparently with shallow, unmargined scrobal depression; length of gena ventrally posterior to eye less than malar space (Fig. 60). Eye at least superficially bare. Antenna (Fig. 58) 13-segmented, scape foreshortened but approximate ratio of segments from pedicel = 4.2: 1.1: 2.4: 2.0: 2.0: 1.8: 1.7: 1.7: 1.7: 5.0; scape compressed, elongate-rectangular for most of length; funicle with 8 segments, fu_1 (Fig. 58: fu_1) differentiated from remaining segments as slightly transverse ring-segment, fl_2 longer than wide and the longest segment, and subsequent segments slightly longer than wide basally to slightly wider than long apically; clava compact 3-segmented with transverse sutures and apparently with only small micropilose sensory region apically on terminal segment. Pronotum in dorsal view (Fig. 59: no_1) about one-third length of mesoscutum with surface sloping from posterior margin, uniformly setose and punctate-reticulate; in lateral view (Fig. 60: no_1) almost vertical with dorsal half only slightly convex. Mesoscutum (Fig. 59) not distinctly shoulder-like posterior to pronotum, about 1.35× wider than long; uniformly convex, setose and punctate-reticulate, without evident parapsidal lines or distinct notauli except apparently for very short furrow (Fig. 60: fur) anteriorly at

level of lateral margin of pronotum mesal to spiracle (Fig. 60: sp). Scutellar-axillar complex with convergent but anteriorly separated, sulcate scutoscutellar sutures (Fig. 59: sss) differentiating low convex axillae and scutellum; sculpture not clearly visible but uniformly setose, including scutellum to posterior margin; axillae equilateral to slightly elongate-triangular with inner angles separated by about 0.5 anterior width of axilla; scutellum not carinate laterally, with distinct frenal arm (Fig. 59: far) but without evident frenum or marginal rim. Metanotum differentiated into median, apparently more or less semicircular dorsellum (Figs 59, 60: dor) and anteriorly crenulate lateral panel; in lateral view obliquely angled dorsellum forming continuous surface with scutellar apex and propodeum (Fig. 60: dor), but in dorsal view scutellar apex and dorsellum separated slightly (Fig. 59). Propodeum without differentiated plical and callar regions, setose lateral to spiracle and with crenulate band along anterior margin posterior to lateral panel of metanotum (Fig. 59); propodeal foramen strongly convergent anteriorly such that propodeum apparently less than half as long medially as laterally and with a median carina; spiracle adjacent to anterior margin laterally (Fig. 59: sp). Prepectus (Fig. 60: pre) triangular with rounded anterior angle projecting anterodorsally in oblique plane relative to mesonotum and extending under spiracle very slightly over extreme posterolateral margin of pronotum to level of anterior margin of spiracle (Fig. 60: sp); dorsal margin extending distinctly posterior to base of tegula and forming almost right angle with posterior margin (Fig. 60). Mesopleuron with uniformly convex acropleuron extending posteriorly to metapleuron (Fig. 60: pl_3) and anterodorsal margin of mesocoxa, at least externally separating linear mesepimeral band (Fig. 60: uep) along posterodorsal margin of acropleuron from flat, triangular, lower mesepimeron between acropleuron and base of mesocoxa (Fig. 60: lep); acropleuron differentiated by crenulate acropleural sulcus (Fig. 60: acs) directed obliquely from above mesocoxa to apex of prepectus, bare, and apparently smooth and shiny; mesepisternum setose ventral to acropleural sulcus (Fig. 60: mes). Metapleuron (Fig. 60: pl_3) superficially a setose triangular region between posterodorsal margin of acropleuron and dorsal margin of metacoxa, but strongly tapered ventrally so as to extend as almost linear, bare strip between acropleuron to anteroventral angle of metacoxa. Mesosternum with sulcate discrimen (Fig. 61: dsc), without transepisternal sulcus, and with straight-transverse posterior margin abutting mesocoxae (Fig. 61: msr). Presence or absence of protibial spicule not visible. Middle leg not conspicuously lengthened, at most about as long as hind leg (Fig. 57); mesocoxa with large basolateral cavity opposite angle formed between acropleuron and mesepisternum (Fig. 61: mcc); mesotibia with strong setae apically, but without differentiated rows of spines (Fig. 64), and with mesotibial spur only about 1.5× as long as apical width of tibia; mesotarsus robust and slightly tapered apically (Fig. 64), the basitarsus only about 3× as long as wide and about as long as remaining segments, the mesotarsal peg pattern not clearly visible but apparently with dense row of spines or pegs along both anterior and posterior ventral margins (Figs 64, 65). Hind leg with tibia and tarsus slender. Fore wing (Fig. 57) hyaline; costal cell setose only along leading margin; basal cell and disc uniformly

setose except for elongate, broad bare band (Fig. 62: spc) behind base of marginal vein and parastigma, bare band separated from venation and basal fold by region of setae about equal to width of bare band; cc: mv: pmv: stv = 5.5: 3.5: 3.0: 1.3; stigmal vein apically curved into distinct uncus. Gaster very broadly sessile, in lateral view (Fig. 63) high with strongly convex dorsal surface, but this an artifact of preservation (tergites and sternites separated, probably due to gas formed during decomposition); with seven visible, uniformly setose gastral tergites; terminal tergite apparently composed of fused Gt_7 and Gt_8, with cercus (Fig. 63: cer) closer to anterior than posterior margin and possibly with suture across tergite anterior to cercus dorsally,



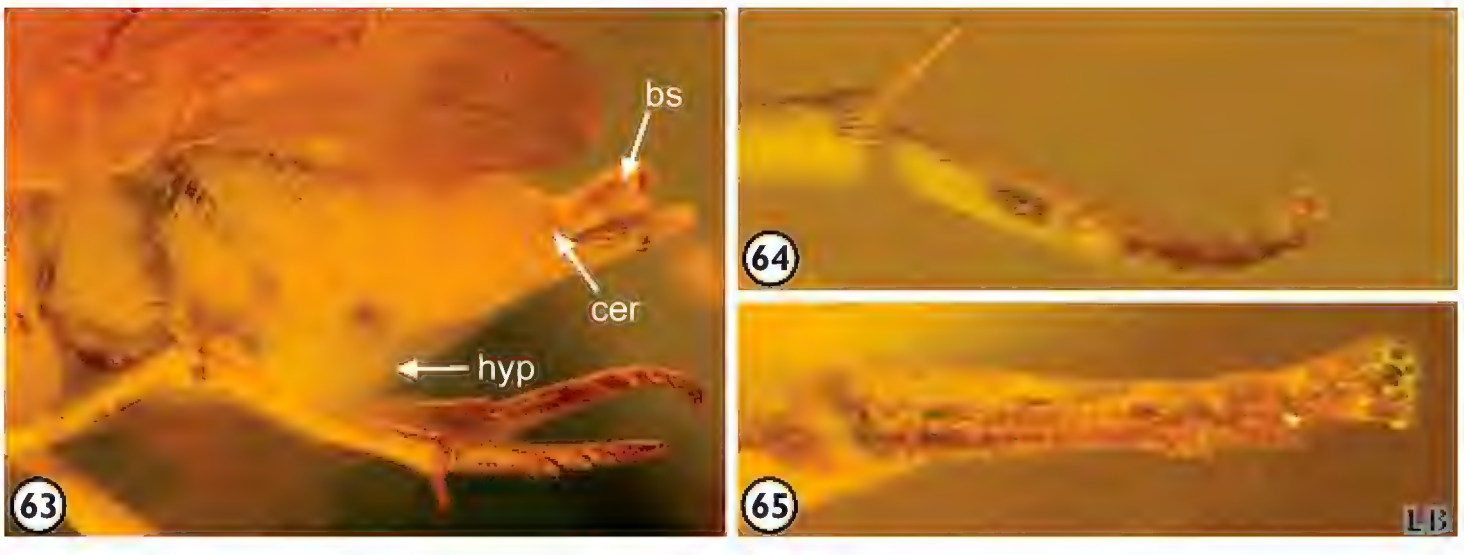
Figures 57–62. *Neanaperiallus masneri* sp. n. (♀ holotype): **57** lateral habitus **58** antenna **59** postero-dorsal head and dorsal mesosoma **60** lateral head and mesosoma **61** ventral mesosternum and mesocoxae **62** base of fore wing.

but at least with deep furrow behind cercus; bare structure (Fig. 63: bs) over ovipositor sheaths posterior to syntergum likely membranous and either extruded anal plate or part of anal filament; hypopygium extending about half length of gaster (Fig. 63: hyp). Ovipositor sheaths projecting, but by distance only about equal to length of basitarsus of middle leg (Fig. 63).

Biology. Unknown, but its short ovipositor sheaths indicate the species parasitized exposed hosts or those comparatively near the surface.

Remarks. *Neanaperiallus masneri* is characterized by most of its setae appearing to be slightly lanceolate or spatulate (Figs 59, 63), but this likely is an artifact resulting from the setae being surrounded by a thin layer of air because in lateral view the pronotal and mesoscutal setae appear more normal (Fig. 60).

In dorsal (Fig. 59) or lateral view (Fig. 60), *N. masneri* has an unusually short and stocky mesosoma compared to the more elongate-fusiform mesosoma that characterizes other Neanastatinae (Figs 1–4, 27, 39, 49) and most other Eupelmidae. Dorsally, this is largely because it has a strongly transverse pronotum and slightly transverse mesoscutum (Fig. 59). In lateral view its enlarged acropleuron also appears to comprise less of the mesosoma than for other Neanastatinae (cf. Fig. 60 with Figs 19, 21, 22, 24, 41, 51) and the ventral surface of the mesosoma is obliquely angled toward the pronotum (Fig. 60) rather than being parallel with the mesonotum as in other eupelmids with a large acropleuron (Figs 19, 21, 22). Likely correlated with its short mesosoma are its relatively short middle legs (Fig. 63), which include a short mesotibial spur and short, robust mesotarsal segments (Figs 64, 65). The middle legs also appear to lack differentiated mesotibial apical pegs and may have more or less uniformly developed spines or pegs along both ventral margins of the mesotarsal segments, though this needs to be confirmed with better preserved specimens. *Neanaperiallus masneri* also has comparatively short antennae (Fig. 58), including a more ring-like first funicular segment (Fig. 58: fu_1). Most Neanastatinae have the first funicular segment elongate, including *Aspidopleura* (Fig. 47: fu_1), though it is quadrate in a few species of *Metapelma* and is conspicuously short and ring-like in *Neanastatus*.



Figures 63–65. *Neanaperiallus masneri* sp. n. (♀ holotype): **63** lateral gaster **64** apex of mesotibia and mesotarsus, lateral view **65** apex of mesotibia and mesotarsus, ventral view.

Discussion

Monophyly and evolution of Neanastatinae. The unique female of *N. masneri* would undoubtedly have been identified as a member of Pteromalidae if it was visible only in dorsal view. This is because structure, setation and sculpture of its pronotum, mesoscutum, scutellar-axillar complex, metanotum, and propodeum (Fig. 59) are all more similar to male Eupelminae (see figs in Gibson 1995) and some Pteromalidae (Gibson 2003, figs 107, 109) than to other Neanastatinae, and because it has a ∩-shaped occipital carina on the back of its head (Fig. 59: oc). Male Eupelminae and all chalcid taxa characterized by a greatly enlarged acropleuron lack an occipital carina. Whether the inner margins of the eyes diverge ventrally cannot be seen, but its antennal structure (8-segmented funicle with a single anellus) is similar to Cleonyminae. Most, if not all, of the similarities between *N. masneri*, male Eupelminae and Cleonyminae likely represent symplesiomorphies rather than synapomorphies, but the absence of linear notauli, a frenum, and a scutellar marginal rim could support a relationship of *Neanaperiallus* with Cleonymini, whereas presence of an occipital carina could support a relationship with Lyciscini. Regardless, classification of *Neanaperiallus* in Neanastatinae suggests this subfamily has a similar type of relationship as was postulated previously for Calosotinae and Eupelminae by Gibson (1989), i.e. it had a common ancestor with Cleonyminae or some clade of Cleonyminae.

Classification of *Neanaperiallus* in Neanastatinae also contradicts several hypotheses of groundplan and autapomorphic states for Neanastatinae made by Gibson (1989), including mesotarsal peg pattern (character 5, state 3), mesoscutal structure (character 7, state 6), presence of elongate-subtriangular axillae with contiguous inner angles (character 11, state 2a), relative structure of the pronotum and mesoscutum (character 12, state 2), presence of mesotibial apical pegs (character 13, state 2), and presence of a linea calva (character 16, state 2). Its classification in Neanastatinae is primarily because the single known female has a conspicuously enlarged acropleuron and non-advanced mesocoxae that cannot rotate anteriorly from their fossae. Consequently, it has the principal apomorphic feature that differentiates Eupelmidae, Encyrtidae and Tanaostigmatidae from other Chalcidoidea, but lacks the apomorphic features that further differentiate Calosotinae, female Eupelminae, Encyrtidae and Tanaostigmatidae from Neanastatinae.

Although *N. masneri* is structurally dissimilar to other Neanastatinae, particularly extant members, it shares some features with *A. baltica*. Both have a very short pronotum (cf. Figs 49, 59 and 51, 60), a crenulate acropleural sulcus that is uniformly curved to near the apex of the prepectus (Figs 51, 60), and a band-like metanotum (Figs 49, 59: dor) with a dorsellum that forms an almost continuous, obliquely angled surface between the scutellum and propodeum (Fig. 60: dor). I hypothesize all of these as symplesiomorphic features relative to other Neanastatinae. Additionally, *A. baltica* shares several other features with one or more other neanastatine genera that I hypothesize as apomorphic. These include having what appears to be the typical mesotarsal peg pattern of extant Neanastatinae and two rows of differentiated spines apically on

the mesotibia (Fig. 56: map), which may be the initial stage in the evolution of a single line of dark pegs that characterize *Brevivulva* (Fig. 43) and all extant genera except *Eopelma*. It also shares anteromedially contiguous, crenulate scutoscutellar sutures (Fig. 49: sss) with *Metapelma* (Fig. 2), *Brevivulva* (Fig. 39) and *Lambdobregma* (Fig. 3), ridged parapsidal lines (Fig. 49: psr) with *Metapelma* (Fig. 2) and *Brevivulva* (Fig. 39), and the axillula developed dorsally into a carina lateral to the scutellum (Fig. 49: scc) with *Metapelma* (Figs 2, 14). The latter two features are unique to Neanastatinae and the character distributions support a hypothesis that *Neanaperiallus*, *Aspidopleura*, *Brevivulva* and extant Neanastatinae except possibly *Eopelma* form a single clade. All features support *Neanaperiallus* as the basal clade of the group except for fore wing setal pattern. The fore wing setal patterns of Pteromalidae and many other Chalcidoidea suggest that a large speculum like that described for *A. baltica* (Fig. 50: spc) is plesiomorphic and therefore likely represents the groundplan structure for the subfamily. The smaller bare band on the fore wing of *N. masneri*, which is separated by setae from the parastigma and basal fold (Fig. 62: spc), more likely represents an independent reduction or intermediate stage in the evolution of a linea calva that characterizes other Neanastatinae (Figs 5–7, 42: lc).

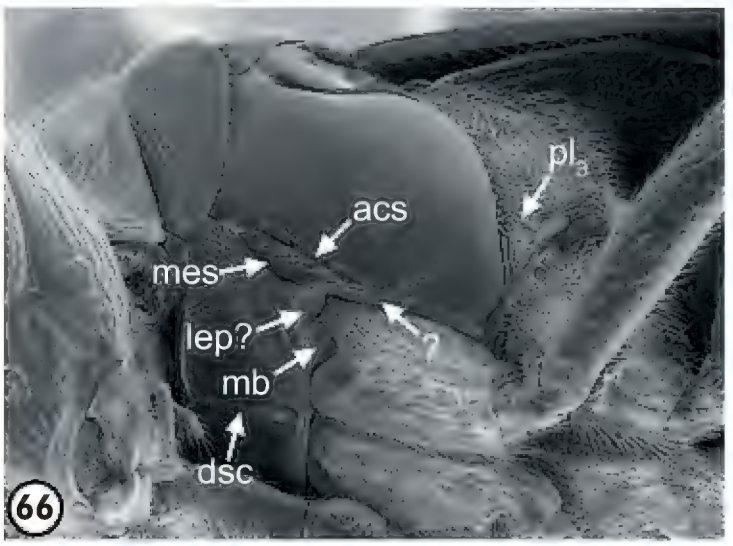
Gibson (1989, character 27, state 2) hypothesized that a hook-like scutellar apex was a synapomorphy for *Lambdobregma* and *Neanastatus*. Individuals of *Metapelma* have the dorsellum projecting under and posterior to the rounded posterior margin of the scutellum as a somewhat concave, V-like surface that is divided by a mediolongitudinal ridge (Fig. 13: dor). The apex of the scutellum, which has a mediolongitudinal groove, is pressed down onto the dorsal surface of the metanotum when the mesonotum is flexed. In *Lambdobregma*, the scutellum projects posteroventrally as a hook-like process over a very slender and slightly concave dorsellum and anteromedial depression of the propodeum (Figs 15, 16). When the mesonotum is flexed the scutellar hook is rotated over the dorsellum into the propodeal depression. *Neanastatus* not only has a hook-like scutellar process that extends over a medially slender dorsellum, but also a hook-like process of the dorsellum that projects over a medially linear and depressed propodeum into a deeply depressed petiole (Figs 17, 18). Both hook-like processes are rotated into the petiolar depression when the mesonotum is flexed in *Neanastatus*. Though the scutellum of *B. electroma* is posteromedially protuberant (Fig. 40: scp), it does not appear to be hook-like and its metanotum is less strongly transverse (Figs 39, 40) than for *Lambdobregma* or *Neanastatus*. Based on the hypothesis that a band-like dorsellum is the groundplan structure for Neanastatinae, one or two transformation series in scutellar-metanotal-propodeal structure are indicated from a *Neanaperiallus*- or *Aspidopleura*-like structure. The structures may constitute a single transformation series (*Neanaperiallus*/*Aspidopleura* → *Metapelma* → *Brevivulva* → *Lambdobregma* → *Neanastatus*) or the structure of *Metapelma* may represent a separate transformation from a band-like dorsellum. Regardless, *Eopelma* differs conspicuously from other Neanastatinae in having an almost flat, transverse-rectangular metanotum that is completely exposed behind the scutellum (Figs 1, 11, 12), including having a median reticulate region (Figs 1, 12: dor) that almost certainly is homologous with a dorsel-

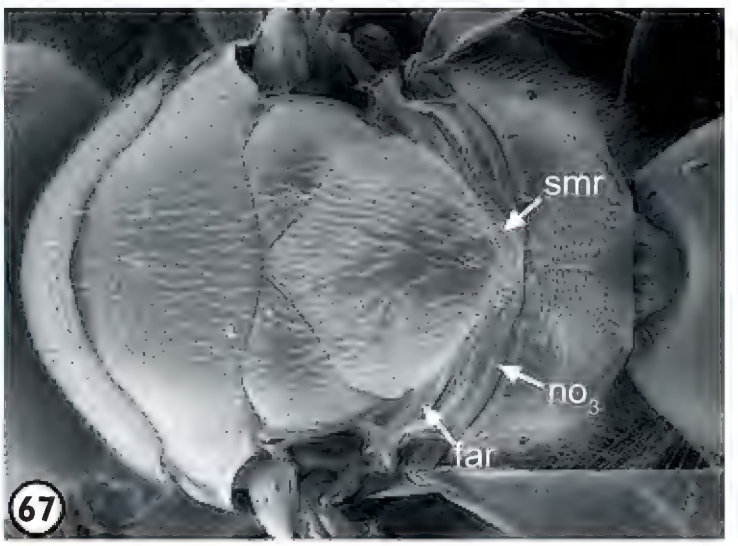
lum. Consequently, the metanotal structure of *Eopelma* is indicated to have evolved independently from a band-like scutellum through the metanotum being secondarily flattened and extended behind the scutellum rather than being overlain by the apex of the scutellum. This supports *Eopelma* as basal to *Brevivulva* and extant Neanastatinae. Gibson (1989) also hypothesized that percurrent parapsidal lines (character 14, state 2) was an autapomorphy of *Metapelma*. However, the presence of ridged parapsidal lines in *Aspidopleura* and *Brevivulva* suggests their presence in *Metapelma* more likely represents a uniquely retained symplesiomorphy among extant Neanastatinae. This revised hypothesis of polarity and hypotheses of scutellar-metanotal-propodeal transformation supports the relationships for extant genera of Neanastatinae given in figure 2a of Gibson (1989), except that *Lambdobregma* is indicated as the sister group of *Neanastatus*.

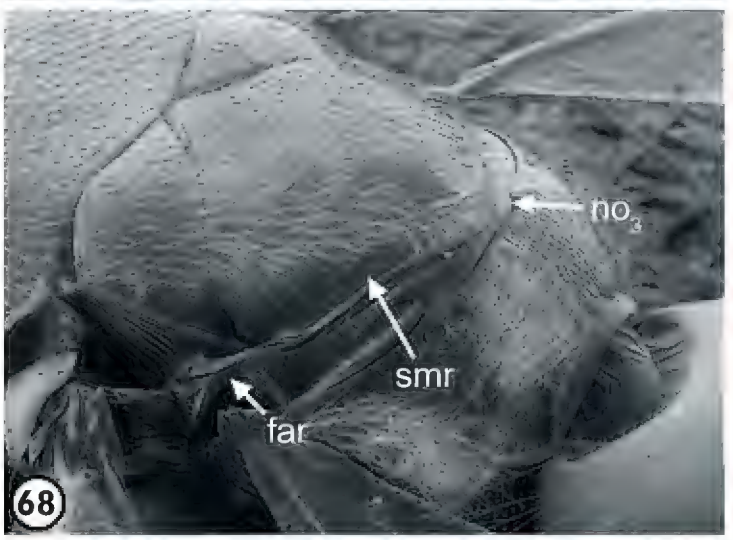
Eopelma has a short mesoscutum (Fig. 1) compared to other Neanastatinae (Figs 2–4, 38, 49) excluding *Neanaperiallus* (Fig. 59). It also has a dorsally extensive, subtriangular pronotum (Fig. 1) and possibly a structure of the acropleural sulcus (Fig. 24) that indicate it is more closely related to *Brevivulva* and extant Neanastatinae than is *Aspidopleura*. Consequently, its comparatively short mesoscutum likely is a result of secondary reduction to retain relative proportions between the dorsal, lateral and ventral surfaces of the mesosoma as its metanotum and propodeum were secondarily lengthened behind the scutellum. However, if *Eopelma* represents a clade that is also basal to *Aspidopleura* then it is possible that its short mesoscutum is symplesiomorphic. Its metanotal-propodeal structure may be the result of secondary lengthening to retain relative proportions between the dorsal, lateral and ventral surfaces of the mesosoma as the acropleuron was further enlarged from a *Neanaperiallus*-like structure (Fig. 60). A relatively basal relationship of *Eopelma* might also indicate that the partly carinate vertex of some species (Fig. 23) represents a secondarily modified occipital carina, and that its comparatively short mesotarsus (Fig. 10) represents a retained symplesiomorphy. Resolution of the structural homology and evolution of the mesopleuron in Neanastatinae would help resolve generic relationships. *Eopelma* has a unique mesopleural structure with a sinuate posteroventral margin of the acropleuron and what appears to be an exposed lower mesepimeron (Fig. 25: lep). This structure could have evolved from a *Neanaperiallus*-like structure (Fig. 60: lep) through further enlargement of the acropleuron. However, neither the mesopleural structures of *Neanaperiallus* (Fig. 60) or *Aspidopleura* (Fig. 51) support the subdivided, convex region between the acropleuron and metapleuron in *Metapelma* (Fig. 20: uep, lep) as being homologous with the upper and lower mesepimeron, as is indicated by musculature. It remains possible that the common ancestor of Neanastatinae had an even less enlarged acropleuron than in *Neanaperiallus* (Fig. 60) and that the different mesopleural structures of Neanastatinae represent multiple independent enlargements.

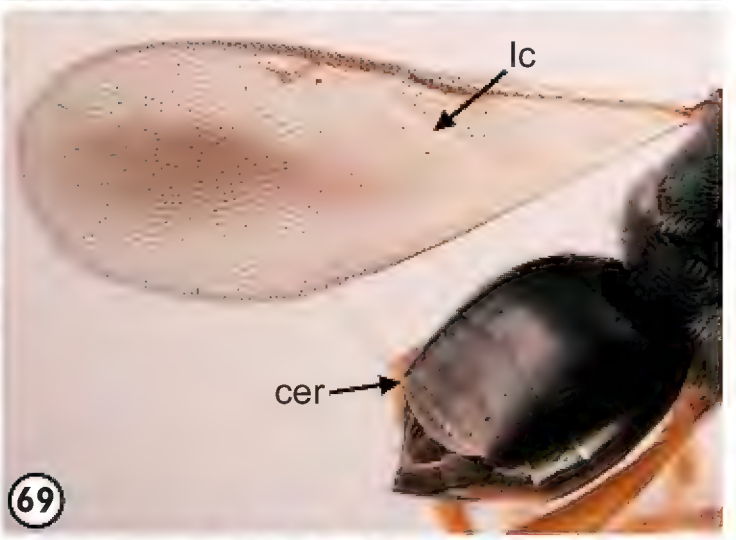
Evidence of relationships with Encyrtidae or Tanaostigmatidae. All members of Encyrtidae and Tanaostigmatidae s. l. have the acropleuron completely enlarged to the metapleuron and there is no evidence that the common ancestor of either family had a pteromalid-like mesosomal structure. Several features suggest that Encyrtidae

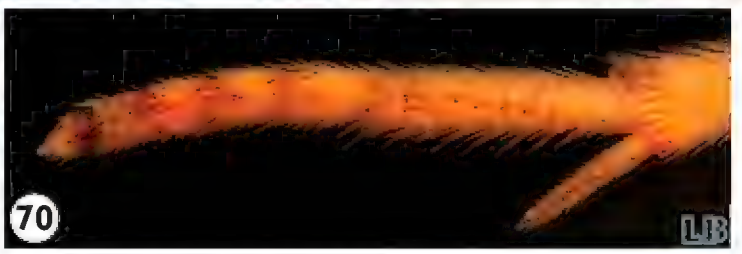
and/or Tanaostigmatidae are closely related to and might even render Neanastatinae paraphyletic if *Neanaperiallus* is classified in the subfamily. Of the three eupelmid subfamilies, only Neanastatinae has a symplesiomorphic mesocoxal structure (non-advanced and unable to rotate out of their fossae), which is similar to that of *Cynipencyrtus* Ishii (Gibson 2008, fig. 43) and *Leptoomus* Gibson (2008, figs 13, 14) (Tanaostigmatidae s. l.), and possibly ancestral to the respective autapomorphic structures of Encyrtidae (Gibson 2008, figs 41, 42) and Tanaostigmatidae s. s. (Gibson 2008, figs 39, 40). Furthermore, Tanaostigmatidae s. l. and Encyrtidae (Fig. 67) are characterized by strongly transverse pronota and a comparatively short and stocky mesosoma. Gibson (1989) hypothesized that these features could have been derived secondarily through reduction from those characteristic of extant Neanastatinae, but the structure of *Neanaperiallus* suggests that they more likely represent symplesiomorphies and could have been inherited from a common ancestor with Neanastatinae prior to subsequent elongation of the pronotum and mesosoma within Neanastatinae.











Figures 66–70. *Savzdargia* sp. (♀): **66** ventrolateral mesosoma **67** dorsal mesosoma and petiole **68** dorsolateral scutellar-axillar complex to petiole **69** fore wing and gaster **70** apex of mesotibia and mesotarsus.

Savzdargia Trjapitzin (Encyrtidae: Tetracneminae) may represent a basal lineage of Encyrtidae (J. S. Noyes, pers. comm.). Among other atypical features for Encyrtidae, *Savzdargia* has unusually long marginal, postmarginal and stigmal veins (Fig. 69) similar to typical Pteromalidae. Like other Encyrtidae it has a completely enlarged acropleuron without any mesepimeron between the acropleuron and metapleuron (Fig. 66). As for most Encyrtidae (Gibson 1998, fig. 51), the acropleural sulcus is continuous anteriorly with the posteroventral margin of the prepectus (Fig. 66: acs), but it does not delimit the posteroventral margin of the acropleuron as in other groups with an enlarged acropleuron (see figs in Gibson 1989 and Figs 19, 21, 22, 24, 41, 51, 60). Rather, in *Savzdargia* the acropleural sulcus is separated from the ventral margin of the acropleuron by a slender region (Fig. 66: ?) along the side of the anteriorly advanced mesocoxa. This slender region is continuous with a small triangular region (Fig. 66: lep?) on the ventral surface of the mesothorax adjacent to the anterolateral margin of the mesocoxa, and with a carina that delineates a lunate region (Fig. 66: mes) between the mesosternum and acropleural sulcus. The lunate region likely is homologous with part of the mesepisternum, but homology of the narrow region along the side of the mesocoxa and of the triangular region anterior to the base of the mesocoxa is more questionable. Other groups with a greatly enlarged acropleuron and non-advanced mesocoxae that have what appears to be a remnant of the lower mesepimeron, such as *Leptoomus* (Gibson 2008, figs 13, 14), *Cynipencyrtus* (Gibson 2008, fig. 43) and some Neanastatinae (Figs 24, 41, 51, 60: lep), have the region between the acropleuron and base of the mesocoxa laterally. Consequently, the triangular region anterior to the mesocoxa in *Savzdargia* may be a remnant of the lower mesepimeron that was isolated as a result of the mesocoxa being secondarily advanced in Encyrtidae. If so, the slender region (Fig. 66: ?) that appears to be part of the acropleuron below the acropleural sulcus likely is an elongation of the lower mesepimeron that is indistinguishably fused with the acropleuron. Such a structure could have been derived from a *Neanaperiallus*-like pleural structure as a result of anterior displacement of the mesocoxae in the common ancestor of Encyrtidae. Within Encyrtidae, *Savzdargia* also has an unusually large, setose metapleuron (Fig. 66: pl_3) similar to that of *Aspidopleura* (Fig. 52) or *Neanaperiallus* (Fig. 60). The mesotarsus of *Savzdargia* also has stronger, rufous spines along the anterior ventral margin of the four basal segments, including a partial double row of spines along the anterior ventral margin of the basitarsus and with the spines arranged obliquely along the anteroapical margin of segments 2–4 (Fig. 70), which I hypothesize as the likely groundplan peg pattern for Neanastatinae excluding *Neanaperiallus*. *Savzdargia* also has a single row of mesotibial apical pegs above the base of the mesotarsus (Fig. 70). Gibson (2008, character 12) stated that although absent from Tanaostigmatidae s. s., mesotibial apical pegs were present in *Leptoomus* and *Cynipencyrtus* (Tanaostigmatidae s. l.). It was not observed that *Leptoomus* has two distinct rows of pegs (Gibson 2008, fig. 19 insert) similar to *A. baltica* and that the apical pegs in *Cynipencyrtus* are variably distinctly aligned into two rows depending on the species (Gibson 1989, fig. 144).

Individuals of *Savzdargia*, like most Encyrtidae, have a slender linea calva (Fig. 69: lc) that is curved toward the base of the wing near its posterior margin similar to *Neanastatus* (Fig. 7), whereas Tanaostigmatidae s. s., *Leptoomus* and *Cynipencyrtus* have a large speculum that is contiguous with the parastigma. Because I postulate this setal pattern as part of the groundplan of Neanastatinae, a linea calva must be convergent in Encyrtidae and Neanastatinae even if they constitute a monophyletic lineage. Clarification of the true groundplan fore wing setal pattern of Encyrtidae could provide additional evidence. Even though most Encyrtidae have a distinct linea calva, fore wing setal pattern is variable and sometimes the bare region is quite broad or even contiguous with the parastigma (e.g. Noyes and Hayat 1984, figs 10, 22, 212, 290, 291) except possibly for a single line of setae (e.g. Noyes and Hayat 1984, figs 30, 107).

Another feature shared between *Savzdargia* (Figs 67, 68) and Neanastatinae excluding *Neanaperiallus* is that the propodeal spiracle is near the midlength of the propodeum. Gibson (2008, fig.11) described the propodeal spiracle of *Leptoomus* as being in the anterior half of the propodeum, but did not note that its posterior margin was very near the midlength of the propodeum, similar to *Aspidopleura* (Fig. 52: sp), or that in *Cynipencyrtus* the spiracle is contiguous with the anterior margin of the propodeum (Gibson 2008, fig. 35), more similar to *Neanaperiallus* (Fig. 59: sp). Relative position of the spiracle is difficult to evaluate unambiguously in most Encyrtidae and Tanaostigmatidae s. s. because the propodeum usually is strongly transverse. Relative position of the propodeal spiracle in Calosotinae and Eupelminae also appears to be variable (see figs in Gibson 1989, 1995) and further analysis is required to determine whether position of the spiracle can be compared adequately among taxa with different shaped propodea.

Unlike most features, relative structure of the scutellum and metanotum appears to be quite consistent for Encyrtidae, at least among macropterous members. Tanaostigmatidae s. s., *Leptoomus* and *Cynipencyrtus* have a band-like metanotum with the dorsellum exposed between the scutellum and propodeum similar to *Neanaperiallus* and *Aspidopleura*, though at least in Tanaostigmatidae s. s. the dorsellum is a very thin vertical sclerite behind the scutellum (LaSalle 1987, figs 92–104). Position of the scutellum relative to the dorsellum also differs slightly in *Cynipencyrtus* depending on whether or not the mesonotum is flexed. The scutellum is slightly protuberant posteriorly and when the mesonotum is not flexed its posterior margin lies above the posteriorly faced vertical surface of the dorsellum, which separates the scutellum from the propodeum. However, the posterior margin of the scutellum is advanced slightly anterior of the posterior margin of the dorsellum when the mesonotum is flexed so that both a horizontal dorsal and the vertical posterior surface of the dorsellum is visible (Gibson 1008, fig. 35). The anterior movement of the posterior margin of the scutellum is a functional consequence of raising its anterior margin during mesonotal flexing, which reduces the length of the mesonotum (Gibson 1986). The scutellum extends to the base of the propodeum over a medially very thin metanotum in *Savzdargia* (Figs 67, 68: no_3) and other Encyrtidae (Noyes 1997, figs 11–18), even when the mesoscutum is flexed (Noyes 1997, fig. 13). Some encyrtids have the apex of the scutellum project-

ing ventrally over the base of the propodeum somewhat similar to *Lambdobregma* (Figs 15, 16) and *Neanastatus* (Figs 17, 18), but metanotal structure differs from these two genera. The frenal arm (Figs 67, 68: far) of the scutellum of encyrtids is also sometimes continued as a rim along the ventral, posterolateral margin of the scutellum, and in *Savzdargia* forms quite a distinct marginal rim (Figs 67, 68: smr) similar to the rim along the posterolateral margin of the scutellum of extant Neanastatinae. The more or less similar dorsellum of *Neanaperiallus*, *Aspidopleura*, *Leptoomus*, *Cynipencyrtus* and Tanaostigmatidae s. s. could represent a symplesiomorphic feature inherited from a common ancestor; however, if Neanastatinae is monophyletic then the posteriorly extended scutellum of Encyrtidae is convergent to that of Neanastatinae. Shape of the axillae of *Savzdargia* (Fig. 67) is similar to that of Tanaostigmatidae s. s. (Gibson 1989, fig. 63). I have not seen a specimen with an arched mesonotum to determine the exact structure of its mesonotal articulation, but based on its scutellar-metanotal structure it likely is similar to other Encyrtidae rather than Tanaostigmatidae s. s.

Combined pronotal-prepectal structure is one feature that could support *Neanaperiallus* having a common ancestor with at least *Leptoomus* + Tanaostigmatidae s. s. Gibson (2008) proposed that the combined pronotal-prepectal structure of the Baltic amber taxon *Leptoomus* might be the groundplan structure from which the superficially quite different pronotal-prepectal structures of Tanaostigmatidae s. s. and *Cynipencyrtus* + Encyrtidae evolved. Among Neanastatinae, the prepectal structure of *Neanaperiallus* (Fig. 60: pre) most closely resembles that of *Eopelma* (Fig. 24) because the dorsal and posterior margins form an almost right angle that results in a truncate posterior margin. In *Aspidopleura* (Figs 48, 51) and most other Neanastatinae the posterodorsal margin of the prepectus forms more of an acute angle (Figs 19, 21) similar to the prepectus of female Eupelminae and Calosotinae (see figs in Gibson 1989, 1995). Individuals of *Neanastatus* are atypical in having a comparatively large and somewhat circular prepectus (Fig. 22) and as in *Eopelma* (Fig. 24), *Cynipencyrtus* (Gibson 1989, figs 47, 48) and many Encyrtidae the dorsal margin is more or less distinctly emarginate at the base of the tegula so that the dorsal or posterodorsal margin extends slightly beyond the base of the tegula. The dorsal margin of the prepectus is also very slightly incised at the base of the tegula in *N. masneri* (Fig. 60), though it extends more conspicuously posteriorly so that at least about the posterior third of the prepectus lies under the tegula similar to *Leptoomus* (Gibson 2008, fig. 11) or Tanaostigmatidae s. s. (Gibson 2008, fig. 38). Furthermore, the rounded anterior angle of the prepectus of *N. masneri* projects very slightly over the posterolateral margin of the pronotum under the mesothoracic spiracle (Fig. 60), whereas it extends to the posterolateral margin of the pronotum in *Eopelma* (Fig. 24) and under the pronotal margin in *Neanastatus* similar to Encyrtidae (Gibson 2008, figs 33, 34). The pronotal-prepectal structure of *N. masneri* (Fig. 60) closely resembles that of *Leptoomus* (Gibson 2008, fig. 11) except that the prepectus is a flat sclerite rather than being convex, lobe-like anteriorly. Even if the slight overlap is an artifact in the unique female of *N. masneri*, its pronotal-prepectal structure is very similar to that hypothesized as ancestral to the pronotal-prepectal structure of at least *Leptoomus* + Tanaostigmatidae s. s. (see Gibson 2008).

Conclusion

Although many of the features discussed above that are shared among some or all of Neanastatinae, Encyrtidae and Tanaostigmatidae s. l. likely represent symplesiomorphies and present conflicting sets of possible relationships, the number of postulated groundplan states shared among the taxa suggests that they are closely related. It is possible that recognition of Tanaostigmatidae and Encyrtidae not only renders Eupelmidae paraphyletic, but that classification of *Neanaperiallus* in Neanastatinae results in one or both families rendering Neanastatinae paraphyletic. There is no compelling evidence that Eupelmidae is monophyletic because each of its three subfamilies may have evolved independently from different cleonymine-like ancestors. Numerically, Encyrtidae is the second most speciose family of Chalcidoidea after Eulophidae (Noyes 2003). Its approximately 460 genera are characterized by extremely diverse mandibular and antennal structures, fore wing color and setal patterns, and body habitus and color patterns, but the mesosomal structures of the seven genera that comprise Neanastatinae are at least as diverse as those of all Encyrtidae. This difference suggests that Neanastatinae constitutes a comparatively old relict clade, whereas Encyrtidae may represent a clade of similar age but one that has diversified explosively. If Neanastatinae is an old clade then the discovery of additional amber fossils will likely increase the number of taxa that can be recognized as distinct genera and should help to further clarify structural transformation series and relationships.

Acknowledgments

I thank Jens-Wilhelm Janzen and David Grimaldi (American Museum of Natural History, New York) for the loan of the amber and John Heraty (University of California, Riverside) and John Noyes (The Natural History Museum, London) for the loan of specimens of *Savzdargia*. I also gratefully acknowledge Ms. Lisa Bartels (CNC) for the scanning electron photomicrographs, photomacrographs, and plates of illustrations, and two anonymous reviewers for their insights on improving the manuscript. This research was conducted as part of the Hymenoptera Tree of Life initiative (National Science Foundation grant DEB-0334945).

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Appendix. Abbreviations used for terms on plates of illustrations

ac	acropleuron
acs	acropleural sulcus
afd	axillar flange (dorsal)
afl	axillar flange (lateral)
axl	axillula
axc	axillar carina
axs	axillular sulcus
bs	bare structure
cer	cercus
cx_2	mesocoxa
das	dorsal axillar surface
dsc	discrimen
dor	dorsellum
far	frenal arm
fra	frenum
fu_1	first funicular segment
fur	furrow
Gt_6	sixth gastral tergite
hyp	hypopygium
iar	interantennal region
lc	linea calva
lep	lower mesepimeron
lmm	lateral margin of metanotum
map	mesotibial apical pegs
mb	membrane
mcc	mesocoxal cavity
mes	mesepisternum
mfp	mesofurcal pit
mpe	metepimeral emargination
mps	micropilose sensory region
msr	mesosternal rim
no_1	pronotum
no_3	metanotum
oc	occipital carina
ovs	ovipositor sheath
pfr	propodeal foramen
pl_3	metapleuron
pg	peg
ppl	propodeal line
pre	prepectus
psp	posterior spines of mesotarsus
psr	parapsidal ridge
ptl	petiole
scc	scutellar carina
scp	scutellar process
set	seta
smr	scutellar marginal rim
sp	spiracle
spc	speculum
ssa	scutoscutellar suture (anterior)
ssp	scutoscutellar suture (posterior)
sss	scutoscutellar suture
sut	suture
tss	transepisternal sulcus
uep	upper mesepimeron